Taxonomic Adjustments in North American Apocynaceae

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ABSTRACT

New combinations in North American Apocynaceae, subfam. Asclepiadoideae are presented and justified: ***Polystemma cordifolium*** (A. Gray) McDonnell & Fishbein, ***Pattalias palmeri*** S. Watson var. ***peninsulare*** (S.F. Blake) Fishbein, and ***Pattalias palustre*** (Pursh) Fishbein. Published on-line www.phytologia.org *Phytologia 99(2): 86-88 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: Asclepiadoideae, *Funastrum*, *Macbridea*, *Matelea*, milkweed vines, *Pattalias*, *Polystemma*, *Rothrockia*, *Seutera*

Several taxonomic innovations are proposed in preparation for the forthcoming *Flora of North America* treatment of Apocynaceae.

Polystemma Decne.

Polystemma Decne. was submerged in *Matelea* Aubl. by Woodson (1941) in his synopsis of North American Asclepiadaceae. His broad circumscription of *Matelea* is widely regarded as a polyphyletic assemblage and *Polystemma* was resurrected by Stevens (2001). Stevens (2001, 2005, 2009) distinguished *Polystemma* from *Matelea* and other related genera by a combination of glandular trichomes that develop white crystalline inclusions with age and smooth, mottled follicles. His circumscription of *Polystemma* corresponds to a monophyletic group in the molecular phylogenetic analyses of McDonnell and Fishbein (unpubl.). Although two new species have been described recently (Lozada Pérez 2010; McDonnell and Fishbein 2016), most of the species belonging to this clade lack combinations in *Polystemma*, as Stevens' revisionary work is ongoing (pers. comm.). One species in the *Flora of North America* region (sensu FNAEC 1993) clearly belongs to *Polystemma* based on the morphological and phylogenetic evidence cited above. The necessary combination is made here.

Polystemma cordifolium (A. Gray) McDonnell & Fishbein, *comb. nov.*
Basionym: *Rothrockia cordifolia* A. Gray, Proc. Amer. Acad. Arts 20: 295. 1885.
Synonym: *Matelea cordifolia* (A. Gray) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

Pattalias S. Watson

Fishbein and Stevens (2005) resurrected *Seutera* Rchb. from the synonymy of *Cynanchum* L. based on a combination of morphological features (umbelliform inflorescences, basally united corona segments) and molecular phylogenetic evidence (Liede and Täuber 2002). However, *Seutera* was published as a replacement for *Macbridea* Raf. and was superfluous and illegitimate at the time of publication (Reveal and Gandhi 2010). Because *Macbridea* Elliott (Lamiaceae) was conserved against *Macbridea* Raf. (Reveal and Gandhi 2010; Brummitt 2011; Barrie 2011), the latter name is also not available in Apocynaceae. Although a proposal was made to conserve *Seutera* against *Macbridea* Raf. (Reveal and Gandhi 2010), this proposal was rejected (Brummit 2011; Barrie 2011). As noted by Fishbein and Stevens (2005) and Reveal and Gandhi (2010), *Pattalias* S. Watson, a largely unused name, is available and should be taken up as the correct generic name for the species placed in *Seutera* by

Fishbein and Stevens (2005). An alternative placement in *Funastrum* was proposed by Liede and Meve (2002). Fishbein and Stevens (2005) rejected this placement on the basis of discordant corona morphology and unsupported molecular phylogenetic evidence. The following synopsis includes all new combinations that are required.

Pattalias palmeri S. Watson, Proc. Amer. Acad. Arts 24: 60. 1889.
Synonyms: *Cynanchum palmeri* (S. Watson) S.F. Blake, Contr. Gray Herb. 52: 83. 1917, not *Cynanchum palmeri* (S. Watson) Shinners, Field & Lab. 19: 65. 1951.
Seutera palmeri (S. Watson) Fishbein & W.D. Stevens, Novon 15: 533. 2005.
Cynanchum mulegense Wiggins, Proc. Calif. Acad. Sci., ser. 4, 30: 247. 1965.

Pattalias palmeri S. Watson var. ***peninsulare*** (S.F. Blake) Fishbein, *comb. nov.*
Basionym: *Cynanchum peninsulare* S.F. Blake, Contr. Gray Herb. 52: 83. 1917
Synonyms: *Cynanchum palmeri* S. Watson var. *peninsulare* (S.F. Blake) I.M. Johnston, Proc. Calif. Acad. Sci., ser. 4, 12: 1129. 1924.
Funastrum peninsulare (S.F. Blake) Liede & Meve, Nordic J. Bot. 22: 589. 2002 [2003].
Seutera palmeri S. Watson var. *peninsulare* (S.F. Blake) Fishbein & W.D. Stevens, Novon 15: 533. 2005.

Pattalias palustre (Pursh) Fishbein, *comb. nov.*
Basionym: *Ceropegia palustris* Pursh, Fl. Amer. Sept. 1: 184, 1813 [1814].
Synonyms: *Vincetoxicum palustre* (Pursh) A. Gray, Syn Fl. N. Amer. 2: 102. 1878.
Cynanchum palustre (Pursh) A. Heller, Cat. N. Amer. Pl. 6. 1898.
Metastelma palustre (Pursh) Schltr., Symb. Antill. 1: 258. 1899.
Lyonia palustris (Pursh) Small, Fl. Miami 149. 1913.
Cynanchum angustifolium Pers., Syn. Pl. 1: 274. 1805, not *Cynanchum angustifolium* Wight & Arn., Contr. Bot. India 57. 1834 or *Cynanchum angustifolium* (Decne.) Morillo, Ernstia 37: 3. 1986.
Funastrum angustifolium (Pers.) Liede & Meve, Nordic J. Bot. 22: 587. 2002 [2003].
Seutera angustifolia (Pers.) Fishbein & W.D. Stevens, Novon 15: 532. 2005.
Amphistelma salinarum C. Wright, Cat. Pl. Cub. 175. 1866.
Metastelma salinarum (C. Wright) C. Wright, Anales Acad. Ci. Med. Habana 105. 1870.
Cynanchum salinarum (C. Wright) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 120. 1955.

Although *Cynanchum angustifolium* Pers. is the oldest basionym applicable to this species, the combination in *Pattalias* is precluded by *P. angustifolius* S. Watson [1889], a synonym of *Metastelma mexicanum* (Brandegee) Fishbein & R.A. Levin.

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Comparison the leaf essential oils of the cultivated fastigiate (strict) growth forms of *Cupressus sempervirens* in California and Turkey

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ABSTRACT

The volatile leaf oils of *Cupressus sempervirens* fastigiate (strict) cultivars from California, USA, and Turkey were analyzed and compared. The volatile leaf oils of cultivated fastigiate growth forms are dominated by α-pinene (27.4 - 65.7%), δ-3-carene (0.2 - 30.1%) and manoyl oxide (0.1 - 9.1%), with moderate amounts of myrcene (2.1 - 2.6%), terpinolene (1.4 - 4.7%), α-terpinyl acetate (1.1 - 4.7%), iso-pimara-7,15-diene (0.3, 1.2%), isoabienol (0.9, 6.0%), and trans-totarol (0.8 - 5.5%). Cedrol was found to be very variable, ranging from none to 7.6%. Cultivars 'Glauca', 'Stricta', 'Tiny Tower', and 'Totem' were each distinct in one or a few components of their oils, but otherwise nearly identical qualitatively and quantitatively. The slight variation in oils (in both California and Turkey cultivars) indicative that there have been multiple selections for the strict or fastigiate habit throughout history. No general suite of compounds distinguished California and Turkey strict cultivars. In spite of the slight differences in the leaf volatile oils, three commercial California cultivars ('Glauca', 'Tiny Tower', and 'Totem') are quite different in their foliage. Published on-line www.phytologia.org *Phytologia 99(2): 89-94 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: *Cupressus sempervirens,* 'Glauca', 'Stricta', 'Tiny Tower', 'Totem', terpenoids.

Cupressus sempervirens L.; referred to as Mediterranean, common, Italian, cemetery, graveyard, or Tuscan cypress; ranges naturally from the eastern Mediterranean, Crete, Cyprus, eastern Aegean Islands, Iran, Israel, Jordan, Lebanon, Syria, Turkey, and possibly Libya (Sękiewicz et al. 2016). Despite having fastigiate (strict) and horizontal forms in the Old World that have been variously taxonomically treated, Farjon (2010) concluded that the widely cultivated fastigiate forms or "cultigens" common throughout the Mediterranean are not a taxonomic variety. The species has been widely cultivated within and outside its range throughout the warm temperate world (More and White 2002). The fastigiate or 'Stricta' form or cultivar is widely planted throughout the world.

The volatile leaf essential oils of *Cupressus sempervirens* have been analyzed based mostly on locally cultivated fastigiate trees. The report by Ulukanli et al. (2014) is typical reporting the major components being: α-pinene (35.6%), trans-pinocarveol (5.22%), α-phellandrene-8-ol (4.56%), β-pinene (3.1%), limonene (2.8%), borneol 2.3%) and camphene (2.2%). Chanegriha, et al. (1977) reported on the leaf oils of *C. sempervirens* from Algeria, likely from a cultivated plant, as having α-pinene (44.9%), δ-3-carene (10.6%), limonene (4.5%), terpinolene (2.7%), terpin-4-ol (1.9%), α-terpinyl acetate (12.0%) and manoyl acetate (1.5%). Floreani et al. (1981) reported the essential oil of cv. 'Stricta' (Argentina) contained α-pinene (50.1%), camphene (1.4%), β-pinene (4.1%), δ-3-carene (30.5%), limonene (3.5%), terpinolene (1.3%) and α-terpineol (1.6%). Other reports are by Adams et al. (1997), Amri et al. (2013), Pauly et al. (1983), Floreani et al. (1982) and Gamero et al. (1978)

Recently, Adams et al. (2017) reported on the leaf essential oils from *Cupressus sempervirens* from both fastigiate and horizontal forms. They found the oils did not differ sufficiently between the two forms to justify the recognition of varieties.

The purpose of the present paper is to report on variation the volatile leaf oils of additional commercial cultivars of the fastigiate forms from California, USA, and compare their oils with those of cultivated trees of the fastigiate forms from Montenegro and Turkey.

MATERIALS AND METHODS

Plant materials:
See Adams et al. (2017) for collection information concerning samples of cv. 'Stricta' from Turkey (*Adams 14597, 14647, 14648, 14675*).
cultivated, Carlsbad, CA, approx. 33° 06' 56.6" N, 117° 18' 39.3" W, 151ft, 17 July 2015, San Diego Co.:
Coll. *Jim A. Bartel 1631,* cv. 'Stricta', Lab Acc. *Robert P. Adams 14591,* oil type I, planted ca. 1985,
Coll. *Jim A. Bartel 1632,* cv. 'Glauca', Lab Acc. *Robert P. Adams 14592,* oil type II, planted ca. 2005,
Coll. *Jim A. Bartel 1633,* cv. 'Stricta' or 'Glauca', Lab Acc. *Robert P. Adams 14593,* oil type I, planted ca. 2000,
Coll. *Jim A. Bartel 1634,* cv. 'Glauca', Lab Acc. *Robert P. Adams 14594,* oil type II, planted ca. 1980,
Coll. *Jim A. Bartel 1635,* cv. 'Glauca', Lab Acc. *Robert P. Adams 14595,* oil type I, planted ca. 2010,
C. sempervirens cv. 'Tiny Tower,' cult. Carlsbad, CA Dec 8, 2016, Coll. *Jim A. Bartel 1637,* Lab Acc. *Robert P. Adams 15057*, planted ca. 2013.
C. sempervirens cv, 'Glauca', cult. Carlsbad, CA, Dec 8, 2016, Coll. *Jim A. Bartel 1638,* Lab Acc. *Robert P. Adams 15058,* planted ca. 2010.
C. sempervirens cv. 'Totem', purchased in 1 gal. container, Green Thumb Super Garden Center, Carlsbad, CA, Dec 8, 2016, Lab Acc. *Robert P. Adams 15059*
All specimens are deposited in the BAYLU herbarium.

Isolation of Oils - Fresh leaves (200 g) were steam distilled for 2 h using a circulatory Clevenger-type apparatus (Adams, 1991). The oil samples were concentrated (ether trap removed) with nitrogen and the samples stored at -20°C until analyzed. The extracted leaves were oven dried (100°C, 48 h) for determination of oil yields.

Chemical Analyses - The oils were analyzed on a HP5971 MSD mass spectrometer, scan time 1 sec., directly coupled to a HP 5890 gas chromatograph, using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column (see 5 for operating details). Identifications were made by library searches of our volatile oil library (Adams, 2007), using the HP Chemstation library search routines, coupled with retention time data of authentic reference compounds. Quantitation was by FID on an HP 5890 gas chromatograph using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column using the HP Chemstation software.

RESULTS AND DISCUSSION

The volatile leaf oils of cv. 'Stricta' are dominated by α-pinene (27.4 - 65.7%), δ-3-carene (0.2 - 30.1%) and manoyl oxide (0.1 - 9.1%), with moderate amounts of myrcene (2.1 - 2.6%), terpinolene (1.4

- 4.7%), α-terpinyl acetate (1.1 - 4.7%), iso-pimara-7,15-diene (0.3, 1.2%), isoabienol (0.9, 6.0%), and trans-totarol (0.8 - 5.5%) (Table 1). Cedrol was found to be most variable ranging from none to 7.6%.

The oils compositions of samples of *C. sempervirens* cv. 'Stricta' or 'Glauca' growing near San Diego, CA, USA proved to very uniform, but two oil types (Type I, II), are seen (Table 1) by their differences in: linalool (0.4%, trace); germacrene D (0.6, 1.6%) and abienol (2.3, 0.7%). Otherwise, the oils are nearly identical. As a group, Types I and II are distinguished from the other California cultivars by their higher amounts of manoyl oxide (7.0 - 9.1% vs. 0.1 - 3.3% in 'Totem', 'Glauca', and 'Tiny Tower,' Table 1).

The oil of cv. 'Totem' is distinguished (Table 1) by high amounts of α-thujene (0.5%), sabinene (5.4%), karahanaenone (0.3%), unknown terpene alcohol (KI1264, 0.2%) and isoabienol (6.0%). In addition, cv. 'Totem' has low amounts of iso-pimara-8(14), 15-diene (0.1%), manoyl oxide (0.1%), and iso-pimara-7,15-diene (0.1%).

The oil of cv. 'Glauca' has no very distinguishing components, except karahanaenone (0.3%) (which it has in common with cv. 'Totem' (Table 1).

The oil of cv. 'Tiny Tower' is distinct by its linalool (2.5%) and camphor (0.3%, Table 1).

Nothing in the leaf oils of the cultivars from Turkey separate them from cultivars in California (Table 1). However, the 'Stricta' Turkey *14597* sample was unusual in having a high concentration of α-pinene (65.7%), and very low concentrations of δ-3-carene (0.2%), linalool (trace), α-cedrene (none), β-cedrene (0.1%), cedrol (trace) and abietadiene (trace).

Jacobson (1996) noted that the introduction of the fastigiate Italian cypress into North America is unknown, but George Washington planted one at Mt. Vernon in 1786. It seems very probable that Italian cypress was introduced into Mexico by the Spaniards much earlier, as it is universally planted at churches and cemeteries in Mexico. Jacobson (1996) lists the introductions of known cultivars as:
cv. 'Glauca Stricta' ≤ 1934; cv. 'Stricta' date uncertain; cv. 'Swane's Golden' ≤1977-78 by Swane Bros. Nursery, Australia; cv. 'Totem' ≤1992, ex Duncan & Davies nursery, NZ; cv. 'Variegata' ≤1930s likely from England ca. 1848.

The commonly cultivated Italian cypress around San Diego, CA appears to be cv. 'Glauca Stricta.' In spite of the slight differences in the leaf volatile oils, the three commercial cultivars ('Tiny Tower,' 'Glauca' and 'Totem') are quite different in their foliage (Fig. 1).

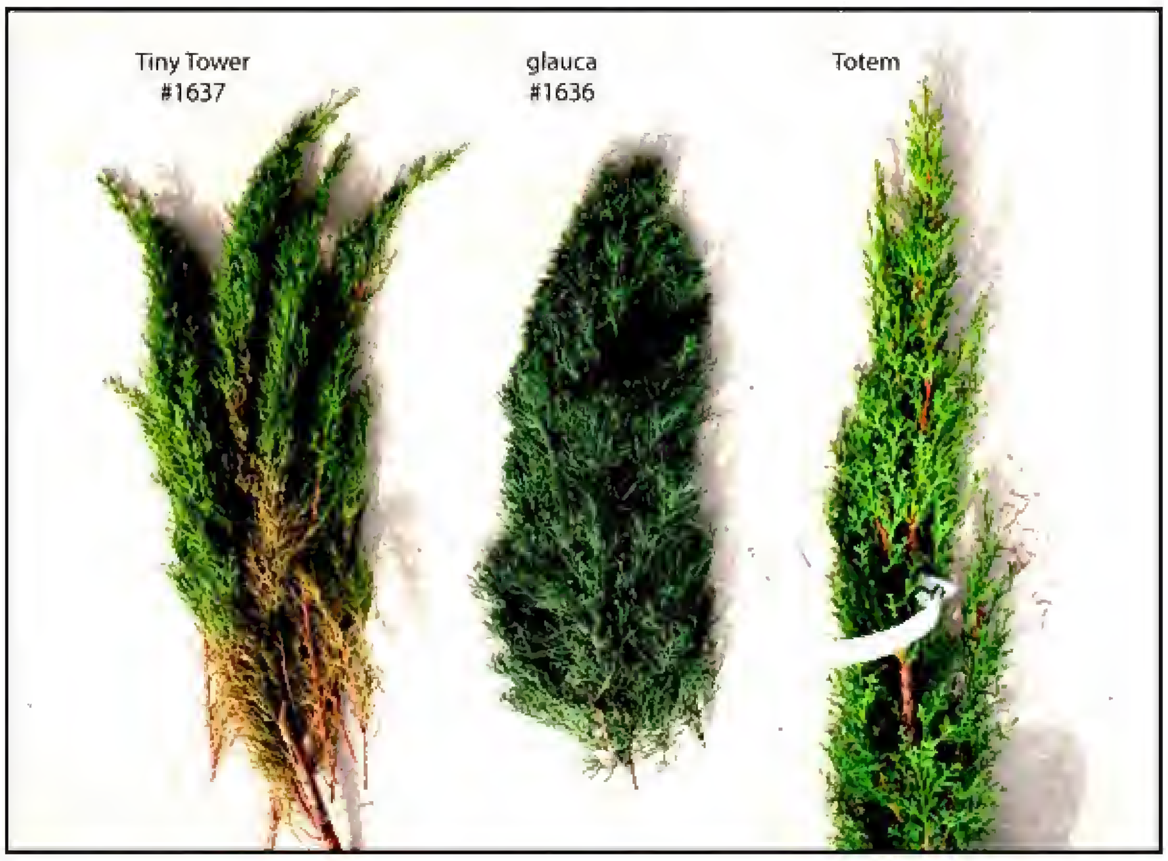

Figure 1. Fresh foliage of cultivars 'Tiny Tower,' 'Glauca' and 'Totem'. Note the variation in color and leaf shapes.

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Table 1. Leaf essential oil compositions for *Cupressus sempervirens* taxa. Compounds in bold show large differences between samples. The oil of Type 1 (14591) was the same as for samples 14593, 14595. The oil of Type 2 (14592) was the same as for sample 14594.

		strict cultivars from California, USA					strict cultivars from Turkey			
KI	compound	Stricta Type 1 14591	Stricta Type 2 14592	cv. Totem 14059	cv. Glauca 15058	cv. Tiny Tower 15057	Stricta Istan. 14674	Stricta Turk. 14647	Stricta Turk. 14648	Stricta Turk. 14597
921	tricyclene	0.1	0.1	0.1	0.1	0.1	0.1	t	0.1	0.1
924	α-thujene	0.1	t	0.5 H	0.1	0.1	0.5 H	0.1	t	t
932	α-pinene	41.2	38.2	27.8	32.5	39.6	34.4	28.5	35.2	65.7 H
945	α-fenchene	0.6	0.5	1.0	0.6	0.7	0.6	0.8	0.9	0.1
946	camphene	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3
969	sabinene	0.7	0.7	5.4 H	0.6	1.0	3.4 H	0.4	0.4	1.0
974	β-pinene	1.1	1.1	1.2	1.0	1.1	1.1	1.1	0.9	1.9
988	myrcene	2.2	2.1	2.8	2.2	2.3	2.4	2.3	2.3	2.6
1002	α-phellandrene	t	t	t	t	t	t	t	t	t
1008	δ-3-carene	17.1	15.8	24.7	18.3	16.5	17.3	30.1	25.7	0.2 L
1014	α-terpinene	0.2	0.1	0.3	0.2	0.2	0.2	0.1	0.1	t
1020	p-cymene	t	t	t	t	t	0.1	0.1	t	t
1023	sylvestrene	0.2	0.2	0.3	0.2	0.2	0.2	0.3	0.3	t
1024	limonene	1.8	2.3	1.4	2.2	2.1	1.0	1.0	0.8	1.4
1025	β-phellandrene	1.3	1.4	1.0	1.5	1.5	0.9	1.0	0.7	1.3
1044	(E)-β-ocimene	0.1	0.2	t	0.1	t	0.1	0.1	0.1	0.1
1054	γ-terpinene	0.3	0.3	0.7	0.3	0.4	0.4	0.2	0.3	0.2
1067	linalool oxide	t	t	0.2	0.1	0.1	t	t	t	t
1086	terpinolene	3.9	4.2	4.7	3.6	3.2	3.2	3.2	4.4	1.4
1099	linalool	0.4	t	0.6	0.5	2.5 H	0.3	0.6	t	t
1118	cis-p-mentha-2-en-1-ol	t	t	0.1	t	0.1	t	0.1	0.1	t
1123	α-camphenal	t	t	-	t	0.1	t	0.1	t	t
1136	trans-p-mentha-2-en-1-ol	t	t	0.1	t	0.1	t	t	t	t
1141	camphor	-	t	-	-	0.3 H	t	t	t	t
1154	karahanaenone	-	-	0.3 H	0.3 H	-	t	t	t	t
1067	umbellulone	-	-	0.5 H	-	-	t	t	t	t
1174	terpinen-4-ol	0.9	0.6	1.8 H	1.0	1.0	0.6	0.6	0.3	0.2
1179	p-cymen-8-ol	t	t	t	t	t	t	0.1	t	t
1186	α-terpineol	0.2	0.2	0.1	0.1	0.1	t	0.2	0.1	t
1204	verbenone	-	-	t	t	t	t	0.2	0.1	t
1241	carvacrol, methyl ether	t	0.1	0.1	0.1	0.1	0.1	0.2	1.0	t
1264	terpene alcohol, FW152	t	-	0.2 H	t	t	t	t	t	t
1287	bornyl acetate	0.2	0.1	0.2	0.2	0.2	0.4	0.2	0.1	t
1295	terpinyl acetate, FW196	-	-	0.2	0.2	0.2	t	t	t	t
1315	<2E,4E->decadienal	0.1	t	0.1	0.2	0.2	t	t	t	t
1334	linalool propionate	0.5	0.4	0.9	0.9	0.9	0.4	1.3	0.7	t
1346	α-terpinyl acetate	2.1	2.1	3.4	4.7	4.7	1.5	4.4	2.8	1.1
1410	α-cedrene	0.1	0.1	NONE	0.1	0.1	0.1	t	NONE	NONE
1411	2-epi-β-funebrene	0.1	0.1	NONE	0.1	0.1	0.1	t	NONE	NONE
1417	(E)-caryophyllene	0.2	0.2	0.1	0.1	0.1	0.2	0.3	t	0.1
1419	β-cedrene	0.1	0.1	NONE	0.1	0.1	0.2	0.3	t	0.1
1448	cis-muurola-3,5-diene	t	0.1	0.1	t	t	0.1	t	0.6	0.2
1452	α-humulene	t	0.1	0.2	t	t	0.2	0.3	t	0.2
1465	cis-muurola-4(14),5-diene	0.2	0.3	0.2	t	t	0.3	0.2	1.5	0.5
1478	γ-muurolene	-	-	-	t	t	t	0.1	t	0.2
1480	germacrene D	0.6	1.6	1.1	0.3	0.3	4.1	1.2	0.6	3.5
1499	epi-zonarene	-	-	-	-	-	t	t	0.6	t
1500	α-muurolene	t	t	-	t	t	t	t	t	0.3
1513	γ-cadinene	t	t	-	t	t	t	t	t	t
1521	trans-calamenene	t	t	-	t	t	0.1	0.1	0.3	0.2
1522	δ-cadinene	t	t	-	t	t	0.1	0.2	0.2	0.2
1550	cis-muurola-5-en-4-β-ol	t	t	0.1	t	t	t	t	t	t
1559	cis-muurola-5-en-4-α-ol	t	0.1	0.1	0.1	0.1	t	t	t	t
1600	cedrol	3.5	5.2	NONE	7.6	7.6	6.2	1.6	NONE	t L
1652	α-cadinol	0.2	0.4	0.3	0.1	0.1	0.4	0.7	1.3	1.3
1685	germacra-4(15),5,10(14)-trien-1-al	0.1	0.2	0.1	0.1	0.1	0.1	1.0	0.3	0.3

		strict cultivars from California, USA					strict cultivars from Turkey			
KI	compound	*Stricta* Type 1 14591	*Stricta* Type 2 14592	cv. Totem 14059	cv. Glauca 15058	cv. Tiny Tower 15057	Stricta Istan. 14674	Stricta Turk. 14647	Stricta Turk. 14648	Stricta Turk. 14597
1930	diterpene, FW272	t	t	0.3 H	t	t	t	t	t	t
1958	iso-pimara-8(14),15-diene	0.5	0.6	0.1 L	0.3	0.3	0.4	0.6	1.2	0.4
1987	manoyl oxide	7.0 H	9.1 H	0.1L	3.3	3.3	0.2	1.3	0.7	2.0
1987	iso-pimara-7,15-diene	1.9	2.7	0.1 L	3.2	3.2	0.2	1.4	0.4	1.3
2055	abietatriene	1.3	1.5	1.7	1.1	1.1	0.5	0.9	1.6	2.5
2087	abietadiene	t	t	0.1	t	t	3.0 H	t	5.4 H	t
2105	isoabienol	1.8	1.8	6.0 H	1.5	1.5	1.4	0.9	0.9	1.2
2149	abienol	2.3	0.7	1.2	1.7	1.7	3.2	0.4	0.8	0.2
2179	abienol isomer	0.2	0.2	0.3	0.4	0.4	t	t	t	t
2269	sandaracopimarinol	0.1	0.1	0.1	0.2	0.2	0.2	t	0.2	t
2282	sempervirol	0.1	0.1	0.3	0.2	0.2	t	t	t	t
2314	trans-totarol	3.0	2.7	3.5	3.0	3.0	5.5 H	1.9	1.4	0.8
2331	trans-ferruginol	0.4	0.4	0.7	0.4	0.4	0.7	0.4	0.2	t

KI = linear Kovats Index on DB-5 column. Compositional values less than 0.1% are denoted as traces (t). Unidentified components less than 0.5% are not reported.

Contrasting perspectives on the measurements and taxonomy of *Arceuthobium* (Viscaceae): a long standing controversy

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ABSTRACT

Kuijt (2016) recently published an exceptionally critical, unsolicited review of two articles on the taxonomic classification of dwarf mistletoes (*Arceuthobium*, Viscaceae:) as well as the methods and morphological characters utilized to delimit taxa. We respond to the criticisms of our methods and conclusions as presented in a paper we recently published in Phytologia on the morphometric analysis of three species in sect. *Campylopoda*: *A. campylopodum*, *A. laricis*, and *A. tsugense*. Kuijt claimed that the foundation of our taxonomic conclusions for these taxa was primarily based on differences in the length of the third internode. This assertion is incorrect. The validity of these species was based on statistical inferences across multiple morphological characters from measurements of both male and female plants. Furthermore, Kuijt inferred that little information is currently available on the susceptibility of hosts to taxa in sect. *Campylopoda*. Again, we disagree and point out that there is a large body of literature demonstrating that there is host preference (i.e., host specificity) among the species of sect. *Campylopoda*—evidence that Kuijt has consistently ignored. The taxonomic classification he has proposed for sect. *Campylopoda* is equivalent to that available in the late 1800's. The implication is that no data relevant to the classification of this group has appeared for over 100 years! We summarized our position on the classification of sect. *Campylopoda* with supporting publications and point out the weaknesses in Kuijt's critique of our work. Research is never complete and additional data are always welcome, particularly from new molecular studies. However, at the present state of our knowledge we will continue to recognize the taxa in sect. *Campylopoda* as species—a classification used by most professional botanists and resource managers for over 40 years. Published on-line www.phytologia.org *Phytologia 99(2): 95-110 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: *Arceuthobium campylopodum*, morphometric analysis, morphological characters, host specialization.

Kuijt (2016) recently criticized the methods and conclusions of an investigation we published the previous year (Mathiasen and Kenaley 2015b) in which we reported additional morphological data for three taxa of *Arceuthobium* (Viscaceae) in sect. *Campylopoda*: *A. campylopodum* Engelmann, *A. laricis* (Piper) St. John, and *A. tsugense* (Rosendahl) G.N. Jones. Because similar unsolicited reviews by the same author have appeared in other journals in the past, but gone unanswered (e.g. Kuijt 1973), we asked the editor of Phytologia to allow us to publish this response.

We need to first point out that Kuijt (2016) began his criticisms of our work with two disclaimers, noting that one taxonomic treatment of sect. *Campylopoda* is no better than another while acknowledging he himself is not an expert in morphometric analysis. Thereafter, he pivoted to a somewhat negative comment, "I shall accept at face value the authentic nature of the techniques employed and the data gathered, and focus on some serious flaws in the claimed *significance* of the mensural [sic] data."

Because Kuijt admitted that he has no expertise in morphometric techniques and the application of modern statistical procedures, his assertion that there are errors in our methods and, hence, our results based on univariate and multivariate statistical analyses must be questioned immediately.

Instead of discussing in detail the many inconsistencies, ambiguous statements, and minor errors in the text of Kuijt's (2016) review of Mathiasen and Kenaley (2015b), we will first provide a brief overview of our past and present work on the taxonomic classification of *Arceuthobium* in sect. *Campylopoda* (for a detailed review see Mathiasen and Kenaley 2016) and, thereafter, focus on what we consider to be the key weaknesses of his criticisms. These include: 1) we do not emphasize nor base our taxonomic conclusions on differences in the length of the third internode of dwarf mistletoe plants; 2) although Kuijt argued that we cannot measure characters to the nearest 0.1 mm accurately, we and others can easily measure the morphological traits selected for comparison of populations to this level of precision using a variety of available equipment; 3) although our "taxonomic judgment" was questioned, we believe our judgment is as sound as the taxonomists who originally described the taxa under debate; 4) we did not emphasize variation in plant color as a major difference between the taxa we studied; and 5) although Kuijt maintained that there are no data available on differences in host susceptibility (i.e., indicative of host specialization) among the dwarf mistletoes we studied, in reality, there is a large amount of data on this subject which has been published and is available to the scientific community.

Taxonomic classification of *Arceuthobium*, section *Campylopoda*

The taxonomic classification of the taxa in sect. *Campylopoda* (*sensu* Hawksworth and Wiens 1972, 1996) has been under debate for many years, as Kuijt (2016) mentioned at the start of his critical review. In the last 20 years, several different classifications have been proposed for these ecologically and pathologically important parasitic plants (Hawksworth and Wiens 1996; Kuijt 2012; Nickrent 2012; Mathiasen and Kenaley 2015a; Nickrent 2016). Because these parasites are among the most serious pathogens of many commercially valuable conifers in Canada, Mexico, and the United States, agreement on a practical and stable taxonomic classification is critical for investigators currently addressing the systematics of this group. Although that may be a laudable goal, additional research, particularly using molecular approaches, will be necessary before it is likely to be achieved as *Arceuthobium* undoubtedly represents a taxonomically difficult genus. Extreme morphological reduction of leaves, flowers, and fruits has limited the morphological characters available for their comparison and study (Hawksworth and Wiens 1996).

Over the last decade, we have collected a large amount of additional morphological data and analyzed it using both univariate and multivariate statistics to provide further insights into the morphological differences among the taxa in sect. *Campylopoda*. In this same time, we have determined the morphological characters contributing most to species differences and, hence, species membership. We have now published several papers presenting our results which we interpreted as supportive of the classification of most of these taxa at the specific level (Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015a, 2015b, 2016: Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). This is the conclusion adopted by Hawksworth and Wiens (1972, 1996) and that which is followed by most professional foresters and forest pathologists in North America who deal with mitigating the damaging effects of these parasites in forest ecosystems (Hawksworth et al. 2002). All of our investigations not only reported statistically significant differences among the means of several morphological characters, but also reported differences in physiological characters (phenology and/or host specificity), which we maintained is further support for the classification of the taxa addressed as separate species or, in some cases, as subspecies. It goes without question that we emphasize the host range of dwarf mistletoes as a major factor in their classification and will continue to do so.

The Issue of Third Internode Length

With regard to Mathiasen and Kenaley (2015b), the major premise in Kuijt (2016) for asserting that our statistical analyses of morphological characters (plant heights, basal diameters, staminate spikes, and flower, fruit and seed dimensions) were all invalid was based solely on our measurement and reported results for the length of the third internode (LTI) among the largest male and female plants from each of the populations under study. His assertion that results related to LTI formed a "major structural part of the taxonomic conclusions" was incorrect. Although we reported LTI data, we never maintained that our taxonomic conclusions were based primarily on statistically significant differences in the mean LTI among taxa. For example, LTI was one of 18 morphological characters examined across female and male plants per population. Although we did indeed report that LTI strongly contributed to determining species membership when comparing female or male plants, we also clearly stated that other female and male morphologies — such as third internode width, seed and fruit length, staminate spike width as well as anther diameter and distance to tip — could be utilized separately or in combination to discriminate among *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*.

As illustrated in Figure 1 (Mathiasen and Kenaley 2015b), the multivariate means and associated 95% confidence ellipses for female (N= 8 characters) and male plants (N= 10 characters) for the aforementioned taxa do not intersect. Our discriminant function analyses clearly demonstrated that these three taxa are morphologically distinct and can be readily distinguished from each other using multiple characters. In addition, our ability to accurately predict species identified *a priori* in the field using only a few characters was exceedingly high (>90%). These three species are among the most morphologically distinct taxa in sect. *Campylopoda* and data on their host affinities also supported this conclusion (Hawksworth and Wiens 1996; Mathiasen and Kenaley 2015b). We are well aware of and will continue to address Kuijt's concerns regarding the efficacy of using the LTI. For example, we have stated this fact in previous work (e.g., page 72 in Mathiasen and Daugherty 2013, page 380 in Mathiasen et al. 2016) and have explained several times our reasons for continuing to report third internode dimensions as well as including these measurements in our morphometric analyses of taxa in sect. *Campylopoda* (Mathiasen and Daugherty 2013; Mathiasen and Kenaley 2015a, 2015b, 2016; Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). Although we do not emphasize LTI as an informative morphological character in *Arceuthobium*, we have discussed in our publications that we believe the combination of comparing basal diameters and the width of the third internode (WTI) among populations is taxonomically informative in that it provided a meaningful comparison of the thickness of plant stems (Mathiasen and Daugherty 2013; Kenaley et al. 2016b; Mathiasen and Kenaley 2015a, 2016). Note that Mathiasen and Kenaley (2015b) summarized the principal characters separating *A. campylopodum*, *A. laricis*, and *A. tsugense* and included WTI, but not LTI (Table 1).

While we are willing to take into consideration Kuijt's assertion that "Seasonal elongation of all internodes can be accepted as a fact in all large species of *Arceuthobium*" (Kuijt 1969), we would prefer to see specific data supporting this assumption rather than the extrapolation of his data from only male plants of *A. americanum* Nuttall ex Engelmann to all other large dwarf mistletoes. To the best of our knowledge, neither he nor other colleagues have reported these data; but we will continue to acknowledge that LTI should not be used as a principal character for the separation of *Arceuthobium* taxa. However, we will also continue to report measurements of this character so our results can be compared with Hawksworth and Wiens (1972, 1996) and with our other investigations to keep the historical record consistent.

Although Kuijt also claimed that we failed to mention the seasons or dates when measurements of third internode dimensions were conducted, these data can be obtained from voucher specimens of *Arceuthobium campylopodum* and *A. laricis* deposited at the Deaver Herbarium (ASC) and the University of Arizona Herbarium (ARIZ) via the public electronic database SEINet (SEINet 2016). Likewise, voucher information for *A. tsugense* can be obtained from the herbarium at the Pacific Research Center, Canadian Department of Forestry, Victoria, British Columbia (DAVFP). Furthermore, we stated that flower measurements were obtained during the peak of flowering for male plants (primarily in August) and during the peak of seed dispersal for female plants (primarily in September) and, of course, this also indicated when all other plant measurements (plant heights, basal diameters, and third internode dimensions) were taken. All of this information is provided in the methods of our Phytologia paper (Mathiasen and Kenaley 2015b).

Accuracy of Measurements and Sampling Bias

As noted previously, Kuijt (2016) emphasized that because we report the mean LTI, this negates the taxonomic usefulness of other characters such as plant heights, basal diameters, and others that he did not define. We completely disagree with his contention and will continue to use these characters to compare dwarf mistletoe plants as others have done for nearly 40 years; see the literature cited in Hawksworth and Wiens (1996) and our publications cited here. Kuijt then implied that we cannot accurately measure morphological characters to the nearest 0.1 mm, an assertion we are sure plant taxonomists and other biologists must find indefensible. As do most investigators who are measuring and comparing small plant structures or microbes (e.g., glumes, lemmas, seeds, pollen, spores, etc.), we defined what equipment was used to measure morphological characters in all of our recent papers: a 7X ocular micrometer and a digital caliper — both of which easily allowed accurate and reproducible measurements to the nearest 0.1 mm. Why Kuijt (2016) finds reporting measurements to the nearest 0.1 mm “dubious” is unclear as he himself has reported morphological measurements for the fruits of several species of *Phoradendron* to the nearest 0.1 mm (e.g., see pages 86 and 96 in Kuijt 2003). Few biologists today would question the ability of investigators to measure morphological characters to the nearest 0.1 mm given the widespread use of ocular micrometers, digital calipers, and stereoscopes. There are many examples of morphometric analyses in the botanical literature and other fields in which investigators measured morphological characters of small plant structures to the nearest 0.1 mm (e.g. Harrison and Hebda 2011; Gardner et al. 2012). Mycologists and bacteriologists commonly measure spores and cells to the nearest 0.1 µm (e.g., Kenaley et al. 2016a). As most taxonomists fully realize, it is a common practice to report the size of morphological characters to the nearest 0.1 mm, or with even greater precision, for many organisms with small morphological characters.

We find Kuijt’s criticism regarding our method of measurement and sampling (Kuijt 2016) incongruous with his own approach to taxonomy as he did not report sample sizes, means, or standard deviations for any of the measurements of morphological characters throughout his monograph on *Phoradendron* (Kuijt 2003); yet, he criticized Nickrent (2012) for not reporting these statistics in the data Nickrent (op. cit.) used from Hawksworth and Wiens (1996) for LTIs. Since Nickrent cited Hawksworth and Wiens as the source of the third internode data, the sample sizes, means, ranges, and standard deviations for third internode measurements he used are accessible in Hawksworth and Wiens (1996, e.g., see page 199 for *Arceuthobium campylopodum*). It appears that Kuijt can hold us and colleagues to one set of standards while following another set that he deems appropriate for his work.

In the same paragraph in which Kuijt (2016) questioned our ability to measure characters accurately to the nearest 0.1 mm, he also criticized our use of flower morphology by maintaining that Nickrent (2012) stated that staminate flower width appeared to show little variation. Although we are unclear what connection there is to measuring staminate flower width to the nearest 0.1 mm and the aforementioned comment by Nickrent on flower width variation, we should point out that Nickrent (2012) relied on flower widths to separate many of the taxa he treats as subspecies of *Arceuthobium campylopodum* — taxa we treat as species. Furthermore, in his treatment of *Arceuthobium* in the Flora of North America, Nickrent (2016) also utilized flower width in his diagnostic descriptions. Evidently, Nickrent (2016) believed staminate flower diameters were consistent enough to use for separating taxa.

Again, we are confident that we, and other biologists, can accurately measure the size of the small flowers of dwarf mistletoes to the nearest 0.1 mm and, if we had chosen to do so, to even smaller precisions using microscopy and image capture technology (Cope et al. 2012). Furthermore, we have demonstrated using univariate and multivariate statistical analyses that mean staminate flower diameters were consistently and significantly different among many species in sect. *Campylopoda* (Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015a, 2015b; Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). Claiming that because we measured the LTI negates the statistical significance of the other morphological characters we used to delimit taxa lacks merit.

Although Kuijt (2016) objected to our sampling of dominant (tallest) plants, we purposefully measured dominant plants on dwarf mistletoe-infected branches in order to standardize measurements of plants within and among populations. It would be meaningless to take a stratified sampling approach comparing the largest to the smallest plants among populations; doing so would require qualitative judgments on plant size(s) that would not be reproducible among populations (or investigators) and inherently would introduce sampling error. The maximum size of the largest plants we measured for *A. laricis* (9.8 cm, 32 populations) never reached the maximum lengths of plants of *A. tsugense*, (16.1 cm, 19 populations) and those of *A. tsugense* never reached the maximum heights observed for *A. campylopodum* (25.4 cm, 60 populations). By sampling and measuring hundreds of the largest plants, we can compare the relative plant size of each taxon over their geographic ranges. Plants must be compared among principal hosts as this is the "environment" in which the plants should reach their maximum growth potential. Thus, it would be meaningless as well to compare plants from less susceptible hosts, particularly rare hosts, as infections most often produce few or no plants. In addition, we always used the mean values for plant heights to detect significant variation among taxa using accepted statistical analysis methods (e.g., analysis of variance and multiple comparison procedures). One of the major reasons we chose to measure dominant plants on infected branches was because Hawksworth and Wiens (1972, 1996) also measured dominant plants for their morphological measurements; this maintained the ability for other investigators to replicate our work and that of Hawksworth and Wiens. Replication of research is dependent on using standardized methods that permit the comparison of results among or between studies. So while Kuijt asserted that the measurement of the dominant plants collected from principal hosts is inappropriate and that color differences are not useful because of environmental influences, we contend that these measurements, among others, provide the best means for standardizing comparisons across the geographic and host ranges of dwarf mistletoes.

The Taxonomic Judgment Paradigm

After criticizing our ability to measure morphological characters accurately, Kuijt (2016) next hypothesized that our measurements were accurate and that the differences among the taxa we compared in our 2015 Phytologia paper (*Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*) were consistent, thereby actually insinuating just the opposite perspective. He then asserted that these same consistent and statistically different morphological discontinuities did not support our conclusion that these taxa should be recognized as species. In support of his claim, Kuijt implied that our "taxonomic judgment" should be questioned on the basis that many living organisms cannot be easily classified using a Linnaean hierarchy. He cited two examples: gulls in the genus *Larus* that constitute what have been termed "ring species," and the Caribbean slipper-spurge (*Euphorbia tithymaloides* L.) which may be an example of a plant that represents a "ring species." Kuijt next stated that he does not believe that the taxa in sect. *Campylopoda* represent an example of a "ring species," so we have not addressed that point in more detail. But why did he inject the concept of "ring species" if he did not believe it was plausible? Thereafter, and without any clear rationale, Kuijt stated that sect. *Campylopoda* could be an example of hybrid swarms (Nolte and Tautz 2010). However, the hybrid swarm analogy is moot when applied to sect. *Campylopoda* as the geographic ranges of many of the species in the section are isolated by hundreds of km and that some are reproductively isolated by differences in flowering period from the rest of the complex (e.g., *A.*

californicum Hawksworth & Wiens; Kenaley et al. 2016b). Even though the geographic ranges and flowering periods of several of the taxa in sect. *Campylopoda* do overlap, there is no published evidence that they hybridize (Hawksworth and Wiens 1972, 1996). However, Nickrent et al. (2004) and Nickrent (2012, 2016) maintained there is also no sound evidence that sympatric taxa in sect. *Campylopoda* do not hybridize. This question needs to be addressed; albeit challenging to prove or disprove sexual compatibility between the taxa (Mathiasen 1982). Thus, Kuijt (2016) ignored the opportunity to provide specific data or at least examples from the literature to support his assertion that taxa in sect. *Campylopoda* might be comparable to hybrid swarms in other plants; without such data and/or supporting literature his assertion that sect. *Campylopoda* taxa might represent hybrid swarms is baseless.

We must also clarify that we did not describe the three taxa in sect. *Campylopoda* examined in our article in Phytologia (Mathiasen and Kenaley 2015b). George Engelmann described *Arceuthobium campylopodum* in 1850 based on plant material collected from ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) from northeastern Washington state (see page 198 in Hawksworth and Wiens 1996). In 1903, R. O. Rosendahl was the first taxonomist to recognize that *A. tsugense* was distinct from *A. campylopodum* and classified it as a species under the genus *Razoumofskya* Hoffman. In 1906, C. V. Piper was the first to recognize that *A. laricis* was morphologically distinct from *A. campylopodum* and warranted separate taxonomic recognition; but he classified it as a subspecies of *Razoumofskya douglasii* (Engelmann) Kuntze. Gill (1935) acknowledged the host susceptibility differences exhibited by these dwarf mistletoes and treated both of these taxa as host forms of *A. campylopodum*: forma *laricis* (Piper) Gill infected western larch (*Larix occidentalis* Nuttall) and forma *tsugensis* (Rosendahl) Gill infected western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent)(and other hemlocks). In 1936, G. N. Jones rejected Gill's host-form concept and recombined *Razoumofskya tsugensis* Rosendahl as *Arceuthobium tsugensis* as the 1930 Cambridge Botanical Congress voted to conserve *Arceuthobium* over *Razoumofskya*. Thereafter, in 1937, H. St. John adopted the use of *Arceuthobium* over *Razoumofskya* and recombined *A. laricis* as a species. Hawksworth and Wiens (1972, 1996) agreed with the classifications of these taxa as *A. tsugense* (not *tsugensis*) and *A. laricis*, summarized their nomenclatural history, and presented morphological, chemical, and host range differences among these taxa which further supported their classification at the specific level.

Our study of these taxa (Mathiasen and Kenaley 2015b) supplemented the morphological data presented by Hawksworth and Wiens (1972, 1996). Moreover, results of our statistical analyses supported the collective conclusions of Piper, St. John, Rosendahl, Jones, and Hawksworth and Wiens that the morphologies of *A. laricis* and *A. tsugense* were sufficiently distinct from *A. campylopodum* to be treated as species. Our investigation of these taxa was partly in response to Kuijt's continued insistence that these taxa, and others in sect. *Campylopoda*, should all be grouped under *A. campylopodum* (Kuijt 2012); a classification that we cannot accept. Furthermore, the vast majority of the professional publications related to *A. laricis* and *A. tsugense* in the last 40 years also recognized them as species (e.g., Smith et al. 1972; Taylor 1995; Beatty et al. 1997; Hennon et al. 2001; Muir and Hennon 2007); a fact demonstrating that resource managers in the United States and Canada who work with these dwarf mistletoes on a professional basis also accept their classification as species. Thus, when casting aspersions on our "taxonomic judgment," Kuijt (2016) also implied that all investigators over the last 110 years who have concluded that *A. laricis* and *A. tsugense* should be classified as distinct species suffer from the same lack of sound judgment. This includes not only the historically well-known plant taxonomists listed above but many other botanists who have classified additional taxa in sect. *Campylopoda* as species; this includes John Coulter, George Engelmann, Philip Munz, Aven Nelson, and Axel Rydberg (Hawksworth and Wiens 1996).

Kuijt's monograph for *Phoradendron* (Kuijt 2003) and his treatment of the Viscaceae for The Jepson Manual (Kuijt 2012) clearly indicated that he follows a typological species concept based mostly on the gross morphology of herbarium collections. The deficiencies of typological methodology have been discussed by many biologists (Mayr 1963; Futuyma 1979; Yoon 2009). The idea dates back to Platonic philosophy and is predicated on a mind-set based on an idealized morphological "type" that places emphasis on the individual, not populations, with the result that variation tends to be either ignored or considered inconsequential (Minkoff 1983). We would add that ecophysiological specialization (host specialization), as well as geographic distributions and barriers to reproduction, are likewise considered to be of little importance in typological classifications. Such a concept abandons the Darwinian paradigm of population thinking and reproductive isolation that has withstood numerous attempts at falsification over the last 150 years (Minkoff 1983).

Plant Color

Although Kuijt (2016) criticized our mention of color differences between *A. campylopodum*, *A. laricis*, and *A. tsugense*, we discussed that only *A. laricis* had distinctively different colored plants (Mathiaen and Kenaley 2015b). However, we agree with Kuijt in general and have pointed out in several papers that plant color is usually an uninformative character for taxonomic classification of *Arceuthobium* (Mathiasen and Daugherty 2009b, 2013; Mathiasen and Kenaley 2015a; Mathiasen et al. 2016). Only when color differences are consistently and remarkably different have we commented on their value as a possible trait to distinguish between taxa (e.g. *A. littorum* Hawksworth, Wiens & Nickrent compared to *A. occidentale* Engelmann; Mathiasen and Daugherty 2013, Mathiasen and Kenaley 2015a). Again, we would maintain that male and female plants of *A. laricis* often can be distinguished from *A. campylopodum* and *A. tsugense* based on color differences. Furthermore, we need to clarify that *A. laricis* is not the taxon occurring near the coast of Washington and British Columbia that Kuijt (2016) claims are greener; this would be a subspecies of *A. tsugense* discussed below.

Host Susceptibility

Kuijt (2016) claimed that we did not address in our Phytologia article (Mathiasen and Kenaley 2015b) the possibility of infrataxon variation in host susceptibility. However, we clearly discussed the major differences in host susceptibility among the three taxa we compared. Thus, to clarify, *Arceuthobium laricis* has not been observed to infect western hemlock (Mathiasen 1998). Mathiasen examined over 800 western hemlocks growing within 6 m of western larch severely-infected with *A. laricis* and found no infection on western hemlock. In addition, Smith (1974) attempted to artificially inoculate western hemlock with *A. laricis*, but no infections resulted. The relative susceptibility of different hosts to dwarf mistletoes is best assessed by quantifying infection on trees growing near severely-infected principal hosts because those trees are exposed to hundreds, if not thousands, of mistletoe seeds annually (Hawksworth and Wiens 1996). It has been demonstrated that one of the principal hosts of *A. campylopodum*, ponderosa pine, is only an occasional host of *A. laricis* (Hawksworth and Wiens 1996, Mathiasen 1998) (see page 43 in Hawksworth and Wiens 1996 for an explanation of the host susceptibility classification system used here: principal, secondary, occasional, and rare hosts). Mathiasen (1998) demonstrated the incidence of infection by *A. laricis* on over 750 ponderosa pines was 15% and plants of *A. laricis* maintained their morphological integrity when growing on this host. Infection of ponderosa pine is easily recognized as crossover infections by *A. laricis*; severe infection is obvious on western larch, while only a few ponderosa pines are infected and seldom are the pines severely-infected. The low level of infection of ponderosa pine by *A. laricis* has also been reported in Canada (Smith et al. 1972). In addition, Smith (1974) successfully inoculated ponderosa pine with *A. laricis*, and although only less than 1% of the seeds placed on trees resulted in infections, 100% of those infections produced aerial shoots. Because *A. tsugense* on western hemlock is not commonly sympatric with western larch there is currently no data on the natural susceptibility of western larch to this dwarf mistletoe (Mathiasen 1994; Hawksworth and Wiens 1996; Mathiasen and Daugherty 2005). However, Smith (1974) successfully inoculated western larch with *A. tsugense*, but only about 7% of the seeds used to inoculate trees produced infections and only 20% of the infections produced aerial shoots. It is essentially impossible to extrapolate the results of artificial inoculations for estimating the relative susceptibility of western larch under natural conditions, but Smith demonstrated that western larch is susceptible to *A. tsugense* to some degree.

No data, of which we are aware, exist that demonstrate genetic differences among ponderosa pine severely infected by *Arceuthobium campylopodum* and those only occasionally infected by *A. laricis* in Oregon, Washington, and British Columbia. Arguing that the much lower level of infection observed and measured on ponderosa pine by *A. laricis* is merely intragenetic variation in host susceptibility of the pine has no merit based on the literature for either this dwarf mistletoe or ponderosa pine. There are no data on the susceptibility of western hemlock to A. *campylopodum* in nature because this tree species is not typically sympatric with ponderosa pine or Jeffrey pine (*Pinus jeffreyi* Greville & Balfour) — the principal hosts of *A. campylopodum*. However, Smith (1974) inoculated two western hemlocks with *A. campylopodum* (50 seeds on each tree) and found that none of the 100 seeds produced an infection. While inconclusive because of the small number of trees Smith inoculated, his research suggested that western hemlock is probably immune to infection by *A. campylopodum*. The apparent immunity of western hemlock to *A. campylopodum* (*sensu stricto*) clearly does not support Kuijt's continued argument that *A. tsugense* and *A. campylopodum* are the same species. However, there is certainly evidence that there is considerable variation in the susceptibility of ponderosa pine and Jeffrey pine to *A. campylopodum* (Scharpf and Roth 1992; Scharpf et al. 1992) and western hemlock to *A. tsugense* (Smith et al. 1993); this variation is the basis for identifying potentially resistant trees to dwarf mistletoes, as well as other plant pathogens.

The fact that Kuijt does not consider host susceptibility differences important is exemplified by his statement "I do not seriously believe host species *per se* make much of a difference, except perhaps sometimes in vigor" (page 6 in Kuijt 2003, and see his discussion of the unimportance of hosts on pages 30-33). Hence, Kuijt has continually ignored much of the scientific literature demonstrating host preference(s) of taxa in sect. *Campylopoda* and continues to do so. It is evident from his arguments that he does not fully understand the contributing factors and processes influencing host-specialization (Kuijt 2003, 2016). The scientific literature is full of examples that have clearly demonstrated the interconnection between host-specific obligate parasites and their hosts (Flor 1971; Brooks and McLennan 1993; Dybadhl and Storfer 2003; Little et al. 2006) including mistletoes (Norton and Carpenter 1998), as well as the factors driving diversification in host-parasite complexes (Barrett et al. 2008). The concept of the host range for a plant pathogen, which includes parasitic plants, is well-accepted in the field of plant pathology and is often applied as a central criterion for species/subspecific delineation of phytopathogenic organisms as "host switching" influences the evolutionary trajectory of the pathogen (Hoberg and Brooks 2008). Not considering the relationships between hosts and mistletoes in the taxonomic classification of the latter, is analogous to ignoring the specialization many plants exhibit for growth on serpentine soils (serpentine indicators/endemics) and the taxonomic classification of those plants as species or subspecies primarily based on their affinity to serpentine (Kruckeberg 1984, Alexander et al. 2007).

Kuijt's (2016) argument asserting that host susceptibility could influence morphological data was based on one photo (Figure 10 in Kuijt 1955) illustrating crossover infections on white spruce (*Picea glauca* (Moench) Voss), a rare host of *Arceuthobium americanum*. The photo illustrated a situation where one white spruce was severely infected whereas another white spruce growing in close proximity was not infected. His argument was unconvincing because this pattern of infection is commonly observed on rare host-dwarf mistletoe combinations. Severe infection of a few white spruce by *A. americanum* with little or no infection of other white spruce growing nearby severely-infected trees has also been reported by Baranyay (1970) and Smith et al. (1972). We have also seen examples of this "all or nothing" infection pattern for other rare hosts of dwarf mistletoes. Thus, there is no "absence of data" as Kuijt (2016) claims on the susceptibility of various hosts to *A. tsugense* (Smith 1971, 1974; Mathiasen 1994; Hawksworth and

Wiens 1996; Mathiasen and Daugherty 2005) and *A. laricis* (Smith 1971, 1974; Hawksworth and Wiens 1996; Mathiasen 1998), but we acknowledge that additional data are needed on the relative susceptibility of several hard pines to *A. campylopodum* (Mathiasen and Kenaley 2015a). However, we have previously observed *A. campylopodum* in mixed ponderosa pine-western larch stands numerous times in Oregon and Washington and, to date, have yet to find a single infection by *A. campylopodum* on western larch. We certainly need quantitative data to support these observations; however, it appears that western larch is immune to infection by *A. campylopodum* in those areas.

We cannot emphasize enough the importance for resource managers to have a taxonomic classification available for *Arceuthobium* that embraces the major differences in host susceptibility that have been observed and/or quantified. Dwarf mistletoe infection has been demonstrated unequivocally to be associated with significant growth losses and premature mortality of severely infected hosts (Hawksworth and Wiens 1996; Hawksworth et al. 2002). Foresters managing dwarf mistletoe populations to mitigate their damaging effects often apply a "species selection" management strategy in mixed-conifer forests infested with one or more dwarf mistletoes. This management approach applies existing knowledge of host susceptibilities to different species of *Arceuthobium* to assist in the execution of forestry operations that shift long-term species composition of infested stands to less susceptible and/or immune conifers. Classifying all of the species we recognize in sect. *Campylopoda* as *A. campylopodum* would mean that nearly all of the trees in each genus in the Pinaceae, except *Pseudotsuga* Carriére, would be a principal host of *A. campylopodum*. Given our own experience and appreciation of the literature demonstrating host affinities in *Arceuthobium*, we currently only consider hard pines to be the principal hosts of *A. campylopodum* (*sensu stricto*) and one of these principal hosts, ponderosa pine, is immune to eight of the species we recognize in sect. *Campylopoda* (Hawksworth and Wiens 1996). Classifying all dwarf mistletoe in sect. *Campylopoda* as *A. campylopodum* would severely hamper the use of "species selection" for the management of these dwarf mistletoes in the western United States and Canada; foresters would be unable to use our knowledge of host susceptibility and grow less susceptible conifers where and when appropriate. We realize that Kuijt is not concerned with this issue, but we know for certain that foresters and forest pathologists routinely apply host distribution(s) in their design and execution of dwarf mistletoe control operations. Thus, resource managers must have a taxonomic system for *Arceuthobium* that acknowledges the host susceptibility differences that have been reported by numerous investigators for over 100 years (Hawksworth and Wiens 1996; Mathiasen and Kenaley 2016).

The populations of *A. tsugense* that Kuijt (2016) discussed parasitizing *Pinus contorta* Douglas ex Loudon in the coastal areas of British Columbia are what most botanists and foresters classify as shore pine (*P. contorta* subsp. *contorta*; Critchfield and Little 1966, Price et al. 1998). These mistletoe populations parasitizing shore pine as a principal host have been classified as *A. tsugense* subsp. *contortae* Wass & Mathiasen (Wass and Mathiasen 2003). The pine often parasitized by *A. laricis* in the interior of southern British Columbia is a subspecies (or sometimes treated as a variety) of lodgepole pine (Rocky Mountain lodgepole pine, *P. contorta* subsp. *latifolia* (Engelmann) Critchfield) which is classified as a secondary host of *A. laricis* (Hawksworth and Wiens 1996, Mathiasen 1998). Although Kuijt considered the classification of *A. tsugense* subsp. *contortae* as "dubious," the distinctiveness of subsp. *contortae* has long been recognized (Smith 1971, 1974; Smith and Wass 1976, 1979; Wass 1976). The dwarf mistletoe on shore pine in southern British Columbia was considered a host specific race of *A. tsugense* for many years (Hawksworth 1987; Hawksworth and Wiens 1996). However, Wass and Mathiasen (2003) classified it as a subspecies based on morphological discontinuities and, particularly, phenological as well as host range differences. Western hemlock is only an occasional host of *A. tsugense* subsp. *contortae* and this level of susceptibility has been clearly documented by Smith and Wass (1976), Wass (1976), and Wass and Mathiasen (2003). Therefore, Kuijt's assertion that both *A. tsugense* and *A. laricis* "not uncommonly parasitizes *Pinus contorta* Dougl. ex Loud., on which it also can perpetuate itself (in at least some coastal locations, surely for many hundreds of years)" is misleading in that he was actually referring to what we consider as two different dwarf mistletoes and botantists specializing on the genus *Pinus* consider two taxonomically different subspecies of *P. contorta*. Kuijt then asked "The pivotal question is: can we distinguish plants in these two different occurrences on *P. contorta*?" The answer to his question is definitively, yes. We can distinguish between *A. tsugense* subsp. *contortae* plants growing on the coastal subspecies of lodgepole pine (shore pine) from those of the morphologically distinct *A. laricis* parasitizing Rocky Mountain lodgepole pine in the interior of British Columbia (Mathiasen and Kenaley 2015b).

Another important counterpoint to note relative to Kuijt's (2016) assertion that morphological data should be collected from non-principal hosts in order to provide convincing evidence for the recognition of infraspecific taxa in sect. *Campylopoda* is that several taxa in this group only parasitize one host. For example, *Arceuthobium abietinum* Engelmann ex Munz f. sp. *magnificae* Hawksworth & Wiens, and *A. californicum* only infect red fir (*Abies magnifica* A. Murray) and sugar pine (*Pinus lambertiana* Douglas), respectively; whereas, *A. apachecum* Hawksworth & Wiens and *A. blumeri* A. Nelson parasitize only southwestern white pine (*Pinus strobiformis* Engelmann) (Hawksworth and Wiens 1996; Kenaley et al. 2016b). Therefore, species of *Arceuthobium* with strictly one principal host precludes the opportunity to make morphological measurements on less susceptible hosts (secondary, occasional, or rare). Furthermore, plants on occasional and certainly rare hosts would not be comparable to plants on principal hosts. Therefore, we will continue to standardize our measurements of dominant plants from only principal hosts for morphological comparisons. However, our studies have already demonstrated some small differences between plant heights on principal hosts and occasional hosts (Mathiasen and Daugherty 2013; Mathiasen et al. 2016), but for some taxa we have found no significant differences between plant heights on different principal hosts (Mathiasen 2011, Mathiasen and Kenaley 2015a). Nevertheless, for the same species of *Arceuthobium*, other characters such as flower dimensions, staminate spike dimensions, and fruit/seed dimensions do not differ significantly on different principal hosts. We believe that the standardization of using the dominant plants for morphological comparisons among principal hosts is the most appropriate methodology, permitting replication of results which can then be cited as supporting or refuting our taxonomic conclusions. Using plants from occasional and rare hosts would bias the results because dwarf mistletoes frequently form few plants on these hosts. However, plants formed on secondary hosts may be acceptable for taxonomic comparisons and this idea deserves further study.

CONCLUSIONS

We have acknowledged Kuijt's concerns regarding the use of the LTI in support of the classification of taxa in sect. *Camyplopoda* (Mathiasen and Daugherty 2013; Mathiasen et al. 2016). Although we have not emphasized LTI to reach taxonomic conclusions, contrary to what Kuijt claimed (Kuijt 2016), we will continue to measure and report third internode dimensions (length and width) because these characters have been reported for dwarf mistletoe since the 1970s (Hawksworth and Wiens 1972) and provide some taxonomic information for comparing different populations of dwarf mistletoes. However, we have not, nor will we ever, base our taxonomic conclusions solely on LTI.

We do not agree with Kuijt's conclusion that no infraspecific classification for sect. *Campylopoda* may be acceptable. The classification of this group by Hawksworth and Wiens (1996), with the addition of a few new subspecies (Wass and Mathiasen 2003; Mathiasen and Daugherty 2007, 2009a; Scott and Mathiasen 2009), has provided a practical and easily applied classification which considers morphological, phenological, and, most importantly, host affinities. Hawksworth and Wiens' classification system has been accepted and is presently used by most professional foresters, forest pathologists, and many botanists who manage these economically and ecologically important parasitic flowering plants.

Adopting a taxonomic classification for sect. *Campylopoda* that does not recognize infraspecific taxa, neither reflects nor advances the totality of knowledge presently available for the designation of species in this group. Kuijt's classification of sect. *Campylopoda* is essentially a classification that sets the taxonomy of this group back to the late 1800s (Kuijt 2012) and is even more unacceptable and impractical than the host-form concept Gill (1935) proposed (Mathiasen and Kenaley 2015a). While we do not agree with Nickrent's (2012, 2016) treatment of most taxa in sect. *Campylopoda* as subspecies of *A. campylopodum*, it is a better approach to this group than that proposed by Kuijt (Kuijt 2012). We believe there are many problems with Nickrent's interpretation regarding the importance of morphological differences and host affinities for classification of dwarf mistletoes, but the principal issues are related to his classification of *A. abietinum*, *A. blumeri*, *A. microcarpum* (Engelmann) Hawksworth & Wiens, and *A. tsugense* as subspecies of *A. campylopodum*. His classification completely obscures the fact that there are cryptic taxa described as subspecies under *A. abietinum*, *A. microcarpum*, and *A. tsugense* (Hawksworth et al. 1992; Wass and Mathiasen 2003; Mathiasen and Daugherty 2007, 2009a; Scott and Mathiasen 2009). Furthermore, we and colleagues, including Nickrent himself, have demonstrated that *A. blumeri* is morphologically and genetically distinct from other dwarf mistletoes that parasitize white pines as well as *A. campylopodum* (Mathiasen 1982, Hawksworth and Wiens 1972, 1996; Nickrent et al. 2004; Reif et al. 2015; Kenaley et al. 2016b). Therefore, we will continue to support the classification of these taxa as species as well as recognize the subspecies that have been delineated under *A. abietinum*, *A. microcarpum*, and *A. tsugense* (e.g. *A. tsugense* subsp. *contortae*). Furthermore, we recommend that botanists, forest pathologists, and foresters continue to apply the Hawksworth and Wiens (1996) classification to dwarf mistletoes as it is the most practical and useful treatment for the management, and when appropriate, conservation of dwarf mistletoes (Mathiasen and Kenaley 2016).

Finally, we cannot agree with Kuijt's (2016) conclusion that "It is advisable to avoid infraspecific categories until the relevant variation patterns of both parasites and hosts are better known, as such categories tend to reflect a deceptive sense of accuracy." Most of the species that have been described in sect. *Campylopoda* were delineated in the late 1800s and early 1900s, over 100 years ago. Additional species and subspecies were described in the late 1960s (Hawksworth and Wiens 1972, 1996). All of these taxa have been accepted by the large majority of resource managers that work with these parasitic plants. There is now a large amount of data relevant to the morphological, phenological, and host range variation for all of the dwarf mistletoes in sect. *Campylopoda*. However, more data are certainly needed, particularly molecular information related to the population genetics of dwarf mistletoes and their hosts. Such open-ended statements as in the first sentence above, obviously leaves us asking exactly what are the relevant variation patterns and how much do we need to know about them before anyone can propose an alternative classification to Kuijt's for sect. *Campylopoda*? Kuijt would have us remain stagnant using a classification dating from the late 1800s instead of synthesizing new morphological and molecular data collected with modern methods and technologies to continually update and improve the classification of *Arceuthobium* in the 21st century and beyond. We prefer to move ahead instead of living in the 19th century with Kuijt.

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Table1. Summary of the principal characters separating *Arceuthobium campylopodum*, *A. tsugense*, and *A. laricis*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers in bold represent key morphological or phenological differences between the taxa. Host susceptibility classification based on information in Hawksworth (1987), Hawksworth and Wiens (1996), Mathiasen (1998), and Mathiasen and Daugherty (2005, 2007). This is Table 2 in Mathiasen and Kenaley (2015b).

Character	***Arceuthobium campylopodum***	***Arceuthobium laricis***	***Arceuthobium tsugense***
Plant height			
Female	**10.4**	**5.3**	**8**
Male	**9.7**	**4.7**	**7.8**
Plant color	Yellow-green, green, yellow-brown	Brown-green, red, purple	Yellow-green, green, yellow-brown
Basal diameter			
Female	**3.4**	**2.4**	**2.7**
Male	**3.2**	**2.1**	**2.6**
Third internode width			
Female	**2.5**	1.7	1.6
Male	**2.5**	1.7	1.6
Staminate spike width	**3.1**	**2.6**	**1.6**
Flower diameter			
3-merous	3.1	**2.7**	3.2
4-merous	**4.2**	3.7	3.8
Fruit length	**5.4**	4.3	4.4
Fruit width	**3.7**	3	2.9
Sympatry among taxa	*A. laricis*	*A. campylopodum*	Not sympatric
Host Susceptibility			
Principal	*Pinus jeffreyi*; *P. ponderosa*	*Larix occidentalis*	*Tsuga heterophylla*
Secondary	*P. attenuata*; *P. coulteri*	*Tsuga mertensiana*; *P. contorta var. latifolia*	None
Occasional	*P. contorta* var. *murrayana*, var. *latifolia; P. sabiniana*	*Abies lasiocarpa*; *Pinus ponderosa*	*Abies amabilis; A. grandis; A.procera; Pinus contorta var.latifolia; Tsuga mertensiana*
Rare	*P. lambertiana*	*Abies grandis*; *Picea engelmannii; Pinus albicaulis; P. monticola; Tsuga heterophylla*	*Picea engelmannii*; *P. sitchensis; Pinus monticola; Pseudotsuga menziesii*
Immune	*Abies grandis*		*P. contorta* var. *murrayana*

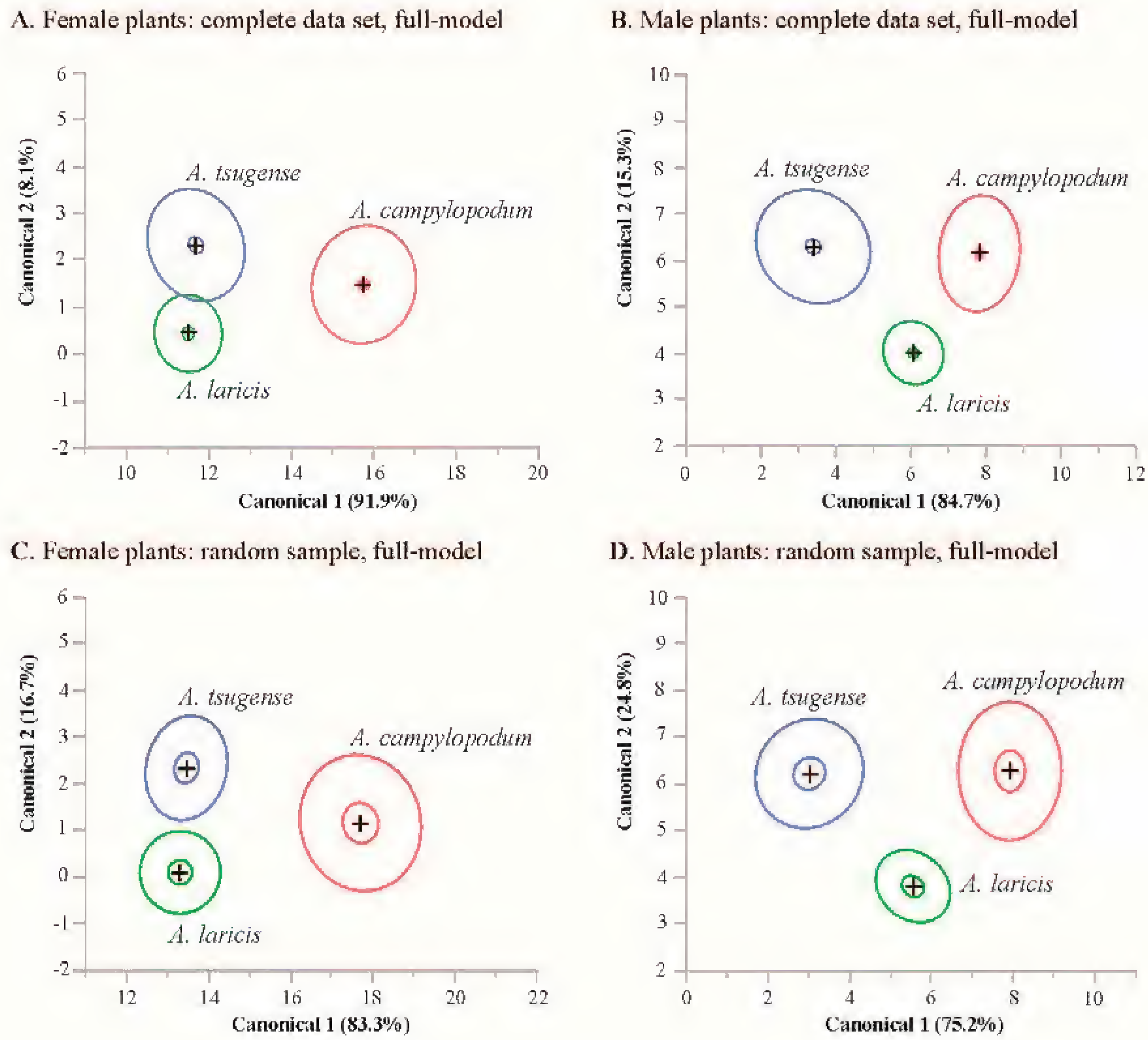

Figure 1. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 6. Multivariate means (squares) were computed using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using a random subset (50 complete records/species) of female (C) and male plants (D), respectively. For each species (A-D), the inner ellipse correspond to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within which 50% of plants for each species reside. From Mathiasen and Kenaley (2015b).

Trifolium hatschbachii (Fabaceae, Papilionoideae), a new species from Argentina, Brazil, and Paraguay

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ABSTRACT

Trifolium hatschbachii, which is similar to *Trifolium polymorphum* and *T. riograndense,* is described as a new species. The new species differs from these in its glabrous foliage, from the former by its lack of cleistogamous flowers, and from the latter by its lack of bracts subtending the inflorescences. It is known from several populations in Argentina, Brazil, and Paraguay. *Trifolium hatschbachii* is named for the late Brazilian botanist Gerdt Guenther Hatschbach. Published on-line www.phytologia.org *Phytologia 99(2): 111-115 (May 9, 2017).* ISSN 030319430.

KEY WORDS: *Trifolium hatschbachii, Trifolium polymorphum, Trifolium riograndense*, Fabaceae, Papilionoideae, new species, Argentina, Brazil, Paraguay

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Species of the genus *Trifolium*, commonly known as clovers, are annual, biennial, or perennial herbs with alternate, palmately (rarely pinnately) compound leaves, most commonly with 3 leaflets. The genus encompasses approximately 240 species (Zohary & Heller 1984), though recent studies by the senior author in New World clovers indicate that there may actually be many more species. Clovers are found in warm to cold temperate environments in both hemispheres, with centers of endemism in Mediterranean habitats (Zohary & Heller 1984). In the flora of South America, there are at least 12 native and 20 introduced species of *Trifolium* (Brako & Zarucchi 1993, Zohary & Heller 1984, Zuloaga et al. 2008).

In the course of reexamination of specimens of the *Trifolium polymorphum* Poir. species complex, several specimens were found from the states of southern Brazil, northeastern Argentina, and southeastern Paraguay which differ markedly from specimens of *T. polymorphum* and *T. riograndense* Burkart, both of which are also native to the region. These differences are spelled out in Table 1. The specimens represent a previously unnamed species, which is described below.

Trifolium hatschbachii Vincent & Butterworth, **sp. nov.** Figures 1, 2. **TYPE**: **BRAZIL**. **Paraná**. mun. Palmas, Horizonte, 3 Dec 1971, *G. Hatschbach 28139* (holotype: C; isotype: MBM).

Similar to *Trifolium polymorphum* Poir. and *T. riograndense* Burkart in their perennial life cycle, stoloniferous growth habit, but differing from them in the following characters: thin, delicate stolons, glabrous leaves; differing from *T. polymorphum* in the absence of cleistogamous flowers and subterranean fruits; differing from *T. riograndense* in the absence of an involucre of bracts below the inflorescence.

Plants perennial; stems branched, prostrate, to at least 50 cm long, glabrous, rooting at the nodes. **Stipules** persistent, 4–12 X 2–5 mm, broadest near the middle, acute or acuminate at the apex, adnate to petioles for half their length. **Leaves** trifoliate; petioles 0.5–4.5 cm, glabrous or with an occasional trichome; leaflets short-petiolulate; petiolules glabrous; leaflets glabrous, sometimes with sparse to dense sessile or stalked golden glands, obcordate, 3.2–8.2 X 4.4–13 mm, margins dentate, base broadly cuneate, apex emarginate, apiculate by the excurrent midvein. **Peduncles** 3.5–11 cm, pubescent or nearly glabrous. **Inflorescences** globose, 1–1.8 cm, 15–25-flowered; bracts lanceolate, 1.5–2 X 0.3–0.5 mm; pedicels 2–3 mm, soon reflexing. **Calyces** five-lobed; tubes 1–2 mm; lobes 1.2–3.1 mm, narrowly triangular, mostly longer than the tubes. **Corollas** pink; banners 4.6–11.3 X 3–7.7, ovate-obovate, apices rounded, emarginate or rarely erose, upcurved from middle when fully expanded; wings spatulate to ovoid, clawed, 3.4–9.3 X 1–3.7 mm, auriculate, apices rounded, smooth or rarely erose, somewhat inflated and convex at maturity; keel petals clawed, 3.4–8.9 X 2.3–4.8 mm, spatulate-elliptic, apices broadly acute or rounded, rarely erose. **Stamens** diadelphous (9+1), 3–7.4 mm, free stamen shorter. **Ovaries** glabrous; ovules 2. **Fruits** not seen. **Seeds** not seen. Flowering at least October to January.

PARATYPES. **ARGENTINA**. Corrientes: Dep. Santo Tome, Estancia "Garruchos", swamp, 22 Oct 1954, *T.M. Pedersen 2937* (C). **BRAZIL.** Paraná: Mun. Campina Grande do Sul, Rio Canguiri, 30 Dec 1969, *G. Hatschbach 23283* (MBM), Mun. Guarapuava, Estrada para Palmairinha, 20 Oct 1960, *G. Hatschbach 7381* (MBM, US); Santa Catarina: Mun. Agua Doce, 28.5 km SE of Horizonte, Parana, Campo de Palmas, *L.B. Smith & R.M. Klein 13455* (NY, R, US), Mun. Bom Retiro, between Fazenda Campo dos Padres and Fazenda Santo Antonio, Campo dos Padres, 21 Nov 1956, *L.B. Smith & R. Klein 7813* (US), *ibid.*, 24 Jan 1957, *L.B. Smith & P.R. Reitz 10405* (R, US); São Paulo: “Bariguey” [Birigui], 29 Oct 1914, *P. Dusen 15773* (GH). **PARAGUAY.** Caaguazu: in region fluminis Yhu, Sep 1905, *E. Hassler 9423* (NY); Guaira: Villa-Rica, 20 Oct 1874, *B. Balansa 1518* (K), Villarrica, *P. Jorgensen 4562* (F, MO, MU).

Trifolium hatschbachii appears to grow in moist sites, since labels describe habitats as swamps, river beds, bogs, but some labels describe the habitat as a field or meadow. Plants of the new species appear delicate in comparison with *T. polymorphum* and *T. riograndense*, which are much stouter overall. The stems are very thin and break easily, as is indicated by the fragmentary nature of most specimens. Leaves of the new species are thin and lack hairs, as opposed to the thicker and very hairy leaves of the other two species. No cleistogamous flowers have been observed on either *T. hatschbachii* or *T. riograndense*, while most specimens of *T. polymorphum* have cleistgamous flowers and fruits that become subterranean at maturity.

The new species is named in honor of Dr. Gerdt Guenther Hatschbach (1923-2013), Brazilian botanist and avid plant collector, who founded the herbarium at the Museo Botánico Municipal (MBM), Curitiba, Brazil (Krapovickas 2013).

Table 1. Differentiating characters of *Trifolium hatschbachii, T. polymorphum,* and *T. riograndense.*

	T. hatschbachii	*T. polymorphum*	*T. riograndense*
Pubescence on leaves	glabrous	pubescent	pubescent
Cleistogamy	absent	present	absent
Involucral bracts	absent	absent	present
Ovule number	2	4	2-4
Midvein excurrent	Yes	No	No

ACKNOWLEDGEMENTS

The authors express gratitude to the curators of the following herbaria for loans of specimens: C, F, GH, K, MBM, MO, MU, R, NY, US. Katy Levings executed the line drawing of the new species. James C. Solomon (MO) provided a copy of Gerdt Hatschbach's obituary. Pre-submission reviews by Thomas G. Lammers (OSH) and Eric J. Tepe (CINC) were very helpful.

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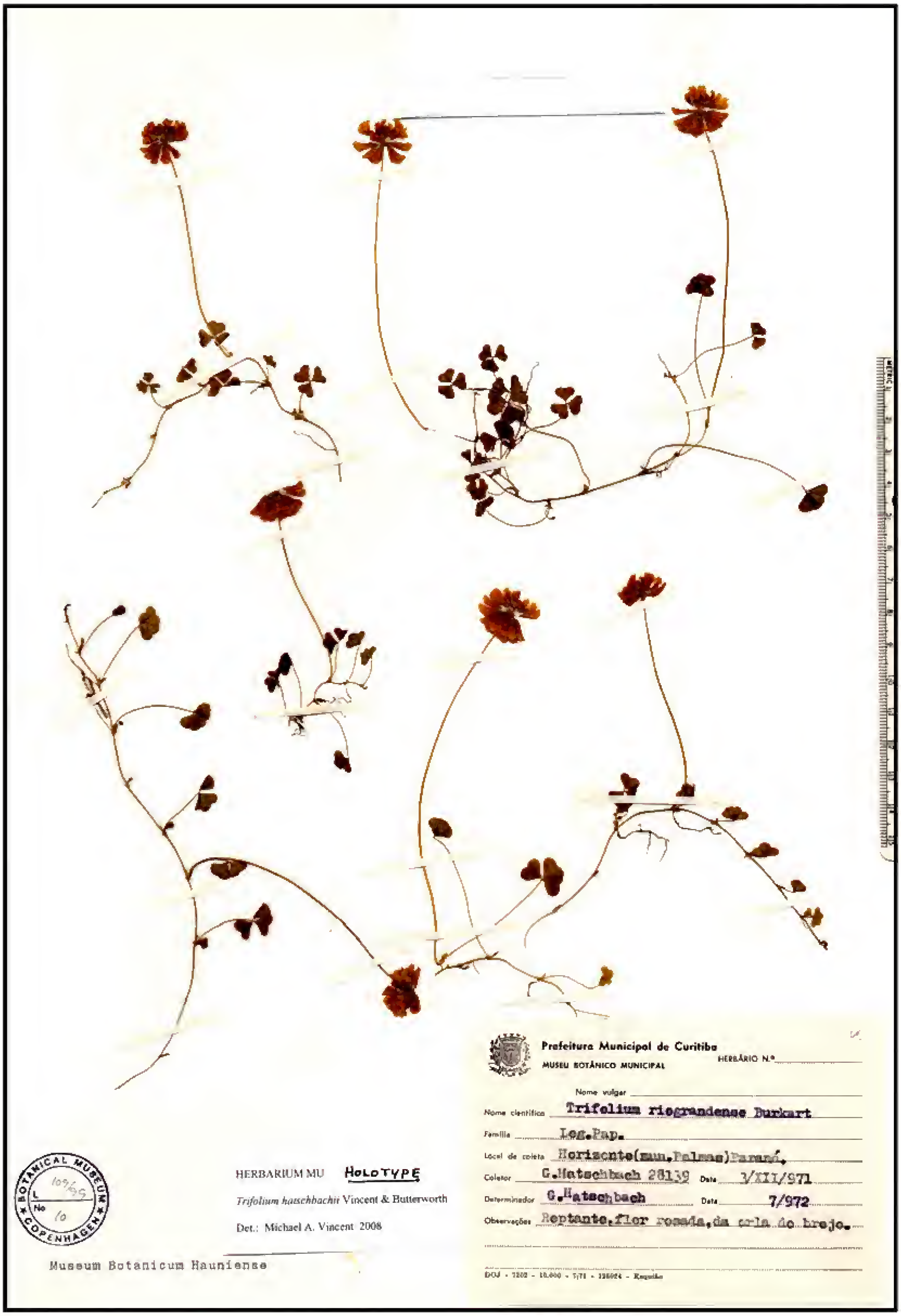

Prefeitura Municipal de Curitiba
MUSEU BOTÂNICO MUNICIPAL
HERBÁRIO N.º

Nome vulgar
Nome científico Trifolium riograndense Burkart
Família Leg.Pap.
Local de coleta Horizonte(mun.Palmas)Paraná.
Coletor G.Hatschbach 28139 Data 3/XII/971
Determinador G.Hatschbach Data 7/972
Observações Reptante,flor rosada,da orla do brejo.

DOJ - 7202 - 10.000 - 1/71 - 126024 - Requião

BOTANICAL MUSEUM ★ COPENHAGEN ★
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HERBARIUM MU HOLOTYPE
Trifolium hatschbachii Vincent & Butterworth
Det.: Michael A. Vincent 2008

Museum Botanicum Hauniense

Figure 1. Holotype of *Trifolium hatschbachii*, *Hatschbach 28139* (C).

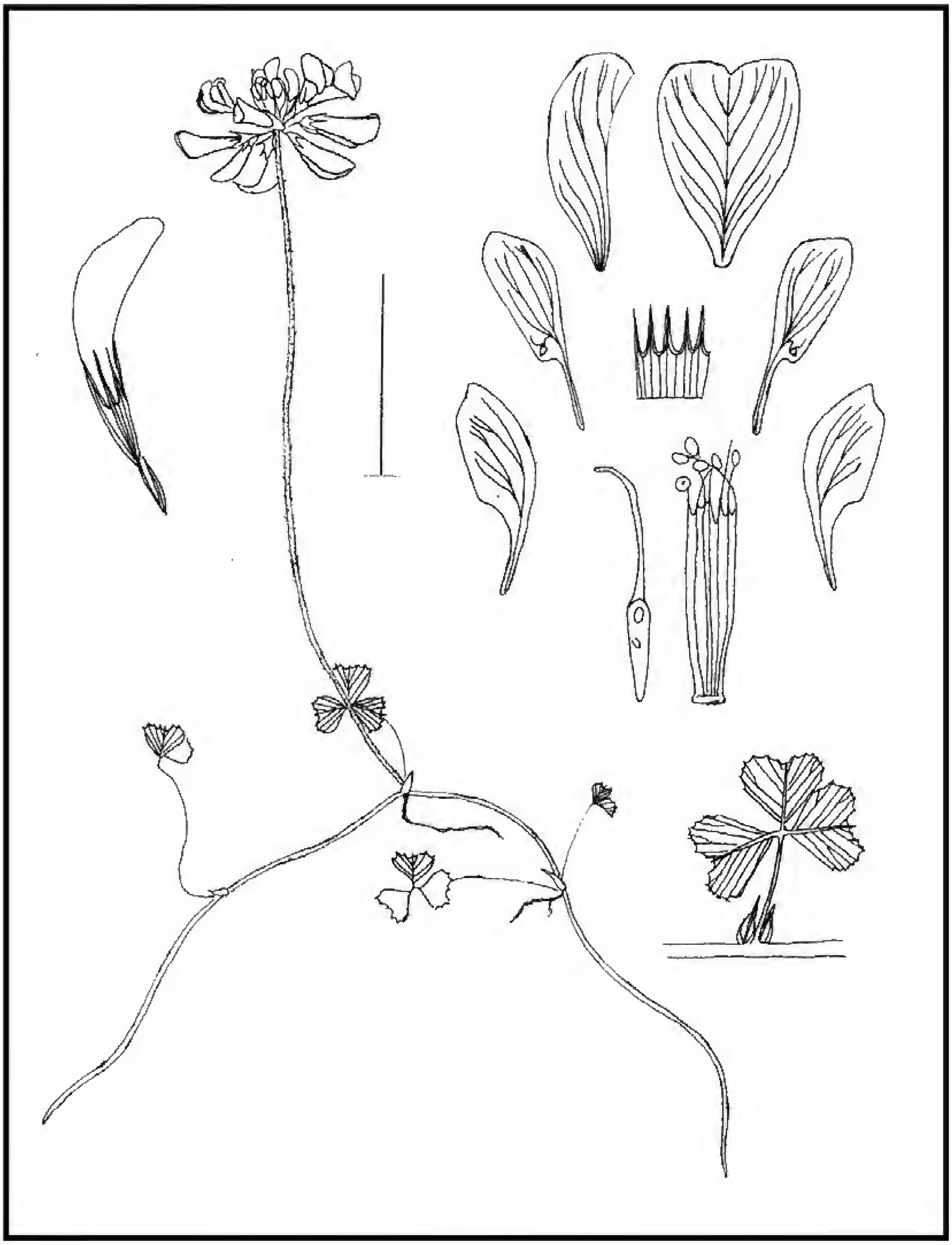

Figure 2. *Trifolium hatschbachii*, line drawing based on the holotype (*Hatschbach 28139,* C). Scale bar: for whole = 3.5 cm; for separate leaf = 18 mm; for whole flower = 6.4 mm; for perianth parts = 10 mm; for staminal column, pistil = 5 mm. Illustration by Katy Levings.

Taxonomic status of *Nama stevensii* var. *gypsicola* (Hydrophyllaceae)

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ABSTRACT

I.M. Johnston first proposed the varietal name *"gypsicola"* positioning it within the well-known *N. hispida*. Bacon subsequently transferred the taxon to the *N. stevensii* complex as var. *gypsicola*. Subsequent workers have largely ignored the name. I have reviewed the problem and conclude that the var. *gypsicola* is synonymous with *N. stevensii* and that there are no obvious morphological characters to distinguish between the populations of the USA and those of northern Mexico. Published on-line www.phytologia.org *Phytologia 99(2): 116-117 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: Hydrophyllaceae, *Nama*, *N. stevensii*, *N. stevensii* var. *gypsicola*.

I. M. Johnston (1941) first proposed the name var. *gypsicola*, a taxon of gypseous soils, the type from southern Coahuila, Mexico. He attached the name to his concept of the widespread, highly variable, *N. hispida*. Bacon (1981) subsequently recognized its much closer relationship to the *N. stevensii* complex of the USA, attaching the varietal name accordingly [*Nama stevensii* var. *gypsicola* (I.M. Johnst.) J.D. Bacon.]

Nama stevensii C.L. Hitchcock is typified by material from Oklahoma. It is also a gypsophile occurring sporatically from southeastern Nebraska to western Texas, and closely adjacent New Mexico (Map1). Populations from Mexico (Map 2), as noted above, have been given the name var. *gypsicola*. Indeed, all of the Mexican specimens of *N. stevensii* at LL-TEX (15 sheets) were annotated as such by Bacon, although he had not published an account of how these might differ from his concept of *N. stevensii* var. *stevensii*, having annotated several sheets as such at LL-TEX.

Strangely, Tyrl et al. (1984), while noting the proposed *N. stevensii* var. *gypsicola* of Bacon, fail to account for its morphological distinction, if any, presumably not having adequate material from Mexico by which to evaluate the proposed taxon. Taylor (2012, unpublished) has provided the most recent taxonomic study of *Nama*. In this she provides an excellent key to the genus *Nama*, the species *N. stevensii* readily recognized from related taxa by its short styles (2-4 mm long). She did however recognize an unpublished taxon (*N. monclova*) having style branches ca 2 mm long (vs 4 mm in *N. stevensii*). She grouped her *S. monclova* next to *N. stevensii* in her cladogram of Fig. A8 (p 225). However, she too does not account for the var. *gypsicola*, apparently sweeping it within the broad confines of *N. stevensii* and/or *N. monclova*, as I have done in the present account: having now examined all of the sheets of both proposed infraspecific taxa at LL-TEX, I conclude that there are no clear morphological characters that separate the named varieties, although there are likely to be DNA differences between the Mexican populations and those of the USA, as suggested by the work of Taylor (2012).

ACKNOWLEDGEMENTS

Disribution maps are based upon specimens on file at LL-TEX and those provided by the website of the USDA. My close colleague, Jana Kos, provided meaningful editorial input.

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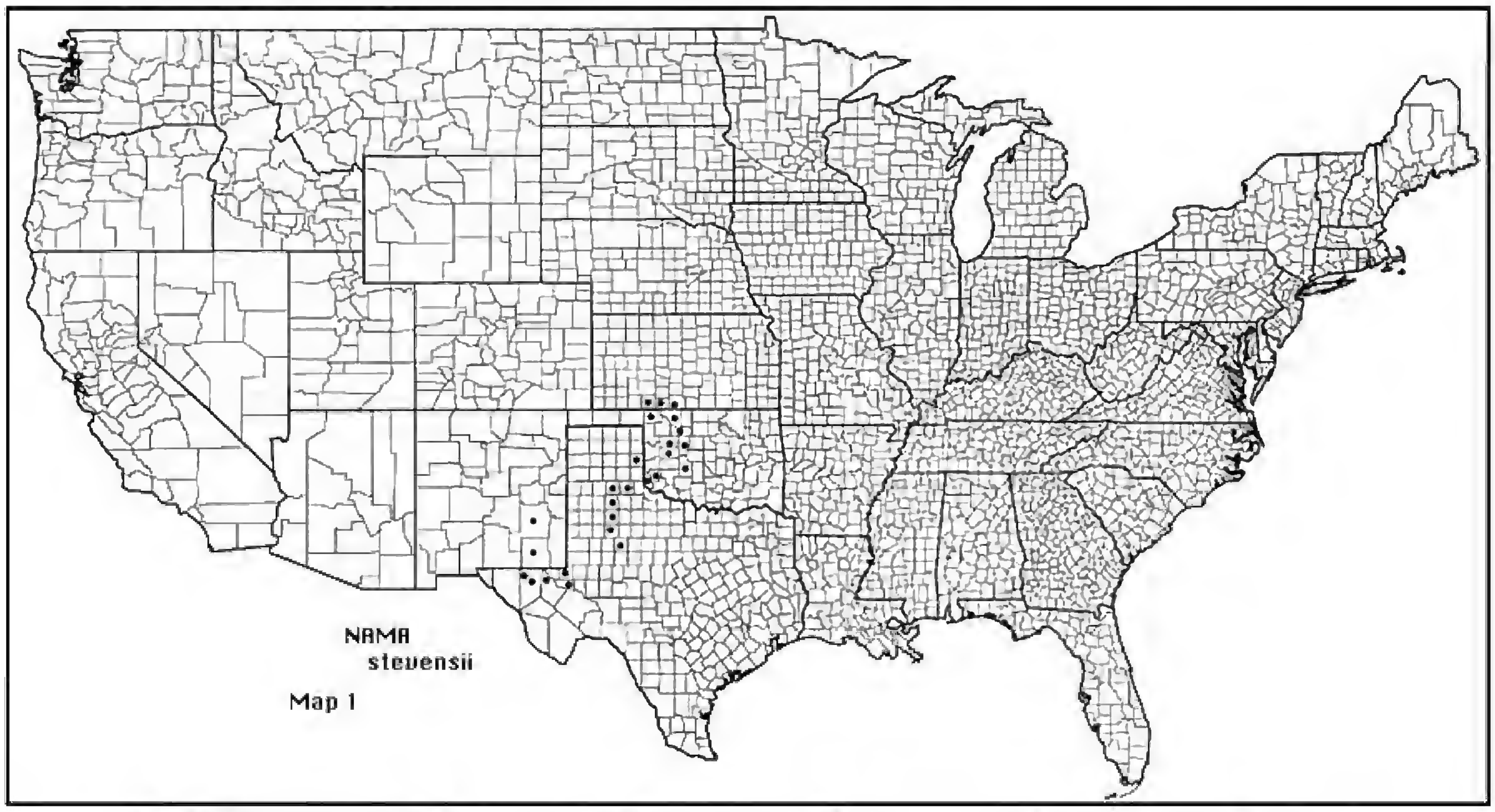

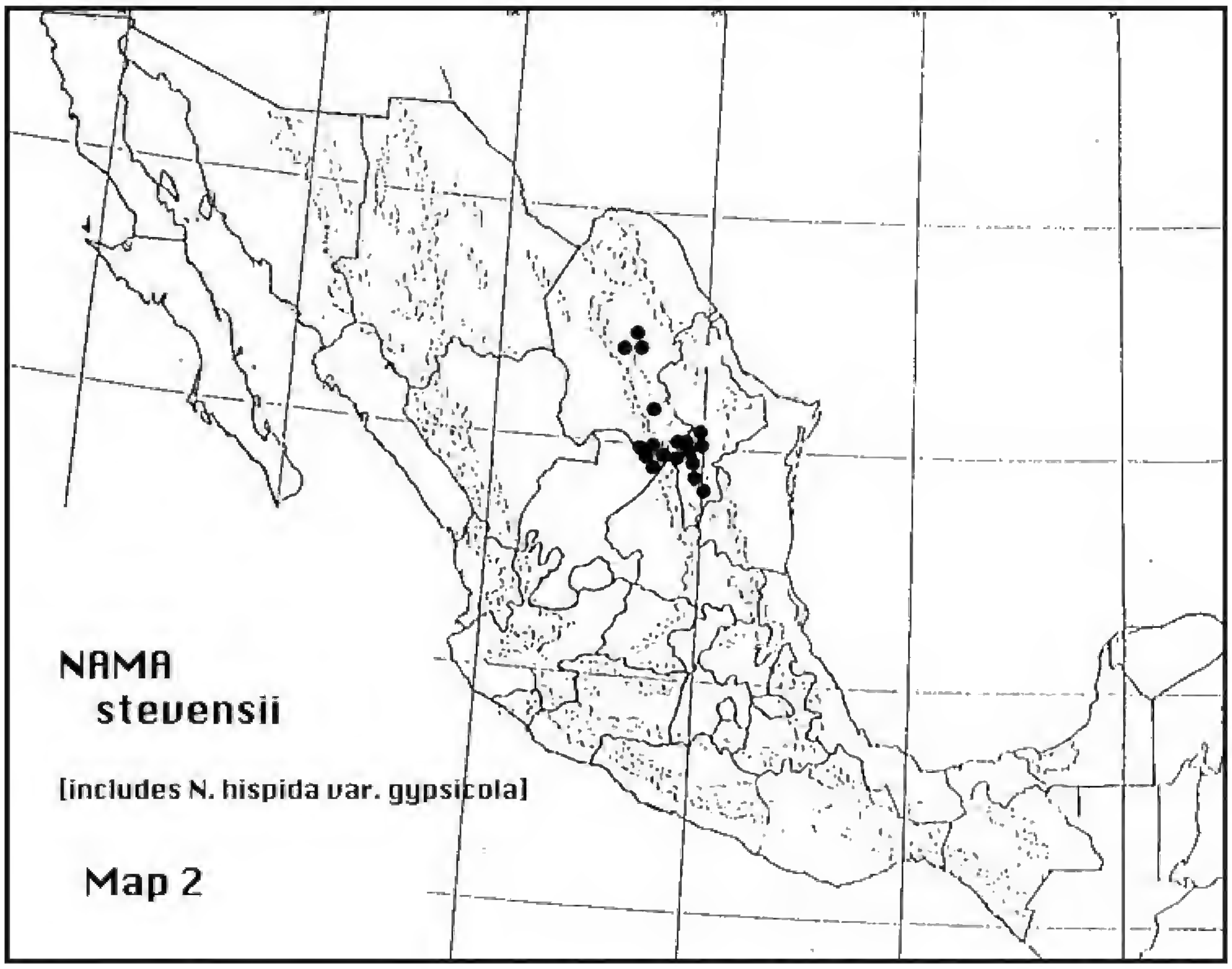

Pollination ecology of the newly described narrow endemic *Ipomopsis ramosa* (Polemoniaceae) in southwestern Colorado

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ABSTRACT

Ipomopsis ramosa is a recently discovered species endemic to a small area of the western San Juan Mountains in southwestern Colorado. The species is closely related to the widespread *I. aggregata* with which it grows sympatrically and appears to be the result of a chance hybrid event between this widespread congener and another species. To understand how reproductive biology may be contributing to the persistence and segregation of *I. ramosa* we completed a series of field investigations to examine the breeding system and pollination dynamics. Our results show that *I. ramosa* is a strictly outcrossing species serviced by two generalist pollinators, *Papilio rutulus* which visits the flowers during its migration early in the season and *Hyles lineata* which serves as the principal pollinator visiting the flowers throughout the flowering season. Floral visitation between both *I. ramosa* and *I. aggregata* was observed; however differences in floral morphology appear to minimize the potential for successful cross-pollination. Published on-line www.phytologia.org *Phytologia 99(2): 118-125 (May 9, 2017).* ISSN 030319430.

KEY WORDS. *Ipomopsis*, Scarlet Gilia, Pollination, Polemoniaceae, Pollinator shift, Pollen analog

Ipomopsis ramosa Schneider & Bregar is a recently described herbaceous biennial endemic to three small side canyons of the Dolores River in Montezuma and Dolores Counties at the western end of San Juan Mountains in southwestern Colorado (Schneider and Bregar, 2011). The species is restricted to south-facing slopes on red sandstones, siltstones, and shale soils of the Permian age Cutler formation and shows an extent of occurrence of 38.9 km^2 and an area of occupancy of 28 km^2 (Bachman et al., 2011). A recent survey (McCauley, 2016) estimates the total occurrence area to consist of approximately 7000 individuals with all populations consisting of a variety of age classes. Across this range the species grows sympatrically with the widespread *Ipomopsis aggregata* (Pursh) V.E. Grant and molecular phylogenetic analysis indicates that *I. ramosa* is likely derived from hybridization of this widespread congener via long-distance pollen dispersal with an as yet unidentified species of *Ipomopsis* (McCauley et al., 2016). Phylogenetic analysis of nuclear ITS sequence data indicates that two rare species *I. polyantha* (Rydberg) Grant and *I. sancti-spiritis* Wilken & Fletcher are the closest relatives to *I. ramosa.* The rarity of these two taxa suggests they may not be the direct progenitor. One species, the widespread *I. arizonica* (Greene) Wherry could be seen as a potential pollen donor due to its similar floral morphology including short styles and included anthers; however further analysis is needed to verify this assumption. Hybridization within the *I. aggregata* complex is common (Grant and Wilken, 1986) and this pattern of inter-specific hybridization via long-distance pollen dispersal has likely given rise to multiple forms inhabiting small areas across the range of the species (Grant and Wilken, 1988).

The small range, potentially recent hybrid origin, and overlapping distribution with *I. aggregata* suggested that further investigation of the breeding system was important for understanding the species' biology and may give insights to its rarity. Differences in floral morphology between the two species suggest different pollinator preferences which may be serving to keep the species distinct (Aldridge and Campbell, 2007; Kishore et al., 2012) and that a pollinator shift may be involved in maintaining segregation of this hybrid derivative (Van der Neit et al., 2014). *Ipomopsis ramosa* has salmon-colored to white flowers with inserted stamens while *I. aggregata* flowers are red and generally express exerted stamens (Schneider and Bregar, 2011) although some higher elevation populations in the region may express inserted stamens. Another potential for maintaining species segregation is the possibility of selfing. While complete autogamy is not reported for the genus *Ipomopsis* and selfing is rare (Grant and Grant, 1965; Waser and Price, 1991) the close relative *I. polyantha* has been shown to set seed via selfing (Collins, 1995) and thus there is potential for expression of that trait in *I. ramosa.* Low seed set due to the hybrid derivative nature of the species (Grant, 1966) or low levels of pollination due to pollinator rarity or inconsistent visitation due to the restricted range (Wilcock and Neiland, 2002) may additionally be limiting dispersal ability.

To evaluate pollination and breeding system ecology of *I. ramosa* we addressed the following specific questions:

1) What is the identity of the principal pollinator(s)?
2) What is the potential contribution of both selfing and outcrossing for fruit production?
3) What is the pattern of pollen movement between *I. ramosa* and the sympatric *I. aggregata*?
4) What are the structural differences between flowers of *I. ramosa* and *I. aggregata* which may be serving to limit gene flow?

MATERIALS AND METHODS

We performed field studies during the summer of 2014 in two side canyons of the Dolores River ca. 38 km northeast of the town of Dolores, Colorado. These two canyons, Roaring Forks Canyon (37°35’13”N, 108°05’44”W) and Wildcat Canyon (37°37’31”N, 108°04’18”W) represent the two largest occurrence areas for *I. ramosa.* Prior observations (Breeden, unpublished data) indicated that flowering begins in late May, generally peaking by mid-July and finishing by mid-August. Field trials and observations were thus timed to span this flowering period.

Breeding system

We tested the potential for selfing vs. outcrossing using pollinator exclusion (Kerns and Inouye, 1993). Thirty individuals in Roaring Forks Canyon were chosen in June prior to anthesis and 15 of these were covered with a mesh of 1 mm diameter. The remaining 15 individuals were left uncovered. From June through August we counted the number of flowers on each individual twice per month. Fruit production was also monitored until maturity. At maturity we collected all fruits intact. Counts of flowers, fruits, and seeds were made for each group and compared using a t-test in SigmaPlot ver. 13.

Pollinator identification

A collective 32 hours were spent in Roaring Forks Canyon spread over different times of the day throughout the flowering period observing and capturing possible pollinators. We captured floral visitors with nets and placed them in a collection jar with ethyl acetate for later identification. To verify insects as pollen carriers, we removed pollen from the proboscis of collected insects, observed it with light microscopy at 1000x, and compared it visually with pollen grains from *I. ramosa.* Due to the similarity in pollen morphology between *I. ramosa* and *I. aggregata* it was not possible to differentiate between the two species.

Pollen movement

To investigate patterns of pollen movement we used florescent dyes as a pollen analogue (Waser and Price, 1982; Fenster et al., 1996; Van Rossum et al., 2010). Four trials were conducted, three in Roaring Forks Canyon and one in Wildcat Canyon in July and August 2014. Slight differences in species abundance were observed between the two sites with *I. ramosa* being the dominant of the two species in Roaring Forks Canyon and *I. aggregata* being dominant in Wildcat Canyon. Fluorescent dye powder (Radiant Color Co., Richmond, CA) was applied to all flowers of 1-2 individuals of each species at peak anthesis growing at central locations within the study area. Each species was painted a different color to assess movement of pollen of each and pigment color was alternated between species at each trial to account for potential pollinator color preference. Dye was applied with a small soft paintbrush to the opening of the corolla and moved downward into the floral tube by gently tapping the flower. Following application of pigment the sites were vacated for 24 hours. Identification of pollen movement was verified by noting the occurrence of dye particles on any flower of an individual plant within a roughly circular area around the dye-source individuals. At Roaring Forks Canyon these circular plots were roughly 150 m^2. Due to a wider spacing of individuals at Wildcat Canyon the plot was larger at approximately 700 m^2. During low light hours each flower within these circular plots was inspected for florescent pigment using a handheld blacklight. Following inspection, the dye-source individuals were removed from the study site and the area given several weeks to purge any remaining pigment before another trial was conducted.

Floral morphology

Twenty flowers of both *I. ramosa* and *I. aggregata* were collected at various locations and elevations throughout Roaring Forks Canyon. These flowers were pressed and dried and measurements taken on the dried flowers of the floral tube, pistil and stamen length. We compared measurements for differences using a t-test in SigmaPlot ver. 13.

RESULTS

Breeding system

The number of flowers produced by both selfing and outcrossing groups was found to not be significantly different (Figure 1). Fruit production however was significantly different between the two groups ($p < 0.0001$) (Figure 1). Seed set was estimated from fruits in outcrossed plants and found to be 3.1.

Pollinator identification

Two pollinators were observed, captured, and confirmed to be carrying pollen of *I. ramosa*. *Papilio rutulus*, the Western Tiger swallowtail, a generalist butterfly in the family Papilionidae was observed on *I. ramosa* in the beginning of June and not noted at any later time (Figure 2). *Hyles lineata*, the Hummingbird Moth, a generalist species of moth in the family Sphingidae was observed visiting *I. ramosa* from mid-June until the middle of August when flowering ceased. Hummingbirds (*Selasphorous spp.*), a common pollinator of *I. aggregata,* were observed in the study area but were not observed visiting individuals of *Ipomopsis*.

Pollen movement

Pollen movement was principally intraspecific although interspecific pollen exchange was observed in all four trials (Figure 3). In each of the three trials conducted in Roaring Forks Canyon, interspecific pigment transfer moved from *I. aggregata* to *I. ramosa*. At Wildcat Canyon, the opposite was true; pigment was transferred from *I. ramosa* to *I. aggregata.*

Floral morphology

Flowers of *I. ramosa* were found to be significantly shorter than those of *I. aggregata* in respect to floral tube length, stamen length and pistil length ($p < 0.01$) (Figure 4). The most evident difference was stamen position. Stamens were found to be included within the floral tube in *I. ramosa* while they were exerted in *I. aggregata*.

DISCUSSION

Our results indicate that seed set in *I. ramosa* requires pollinator visitation and does not exhibit the potential for selfing as seen in its close relative *I. polyantha* (Collins, 1995). The low level of seed set seen in the pollinator exclusion experiment is likely the result of rare chance pollination due to a loose fitting bag covering an inflorescence. This indicates that while *I. ramosa* is likely of hybrid origin this did not lead to the evolution of self-fertility. While the action of a pollinator is required for seed set our experiment did not differentiate between pollen exchanges among flowers of the same individual and thus the potential for geitonogamy cannot be fully ruled out. Further examination via manipulation of floral structures would be necessary to evaluate this question.

The two floral visitors observed on *I. ramosa* were both generalist, polylectic species which have been commonly reported visiting species of Polemoniaceae, including *Ipomopsis* (Grant and Grant, 1965). *Papilio rutulus*, only observed for a short period of time in June, is a migratory species making significant movements at various times during the summer months (Scott, 1986). While not likely serving as the principal pollinator due to its short time in the population this species is likely important as it could serve as a vector for long-distance pollen movement connecting this endemic species with others across a wide area. This potential for long-distance pollen movement and subsequent cross-pollination has been invoked as a plausible mechanism for the recent origin of this species (McCauley et al., 2016).

Hyles lineata, which we observed visiting the population for an extended period of time during most of the flowering period is a local resident species. This species likely serves as the principal pollinator of *I. ramosa*. Based on floral form and general pollination syndrome this should serve to isolate *I. ramosa* from *I. aggregata* and provide evidence for a pollinator shift in the evolution of *I. ramosa*. *Ipomopsis aggregata* with its red tubular flowers is principally pollinated by hummingbirds (Grant and Grant, 1965) although various Sphingidae species, including *H. lineata* are often seen associating with and occasionally pollinating it (Juenger and Bergelson, 1997). While *H. lineata* will more often associate with lighter white to pink flowers the species has been shown to act as a generalist, particularly in high elevation areas. This is mostly driven by the coldness of the areas limiting *H. lineata* activity at night when light floral colors are most distinct to the pollinator (Aldridge and Campbell, 2007). Thus while *I. aggregata* is likely being pollinated by hummingbirds, and we did observe hummingbird (*Selasphorous spp.*) activity in the area of Roaring Forks Canyon, floral visitation is being made by *H. lineata* providing the possibility for pollen exchange.

The examination of pollen movement between *I. ramosa* and sympatric *I. aggregata* indicated the occurrence of pollen exchange between the two species. All trials indicated that interspecific movement while less common than intraspecific movement, did occur. This greater frequency of intraspecific pollen movement suggests that there may be pollinator preference and division based on the servicing pollinator. Interspecific pollen movement was likely facilitated by the generalist behavior of *H. lineata*. Floral preference by *H. lineata* cannot be evaluated here as pollinator observations were not made on *I. aggregata* but assuming patterns seen by other Sphingidae *I. aggregata* would be of secondary preference to the lighter colored *I. ramosa*. Assuming however that *H. lineata* may not show any preference between the two species of *Ipomopsis* the same pattern of pollen flow could be explained by the pattern of clumping that the species exhibit in the field. Nearest-neighbor visitation may be the principal explanation for the observed pattern. Further pollinator observations are needed to differentiate these two driving forces behind the observed pattern of interspecific pollen flow.

Morphological analysis indicates that mechanical isolation in the form of floral structure is an important mechanism for isolation of *I. ramosa*. Evidence points to some floral traits in *Ipomopsis* being under relatively simple genetic control and thus these differences could have evolved relatively rapidly (Wolf and Soltis, 1992). With the potential for pollen flow between *I. ramosa* and *I. aggregata*, differences in morphology, particularly the placement of stamens and stigmas, may be preventing cross-pollination. The differences in stamen and stigma insertion however suggest a potential for asymmetric pollen flow with *I. ramosa* having inserted stamens being able to fertilize *I. aggregata*, but *I. aggregata* not being able to fertilize *I. ramosa*. Such asymmetrical differences in pollen movement have been previously observed in other closely related and hybridizing members of *Ipomopsis* (Wolf et al., 2001) and play important roles in pollen transfer. If this apparent pattern stands up it would mean that *I. ramosa* can be maintained as a genetically isolated population and may be able to spread via introgression with *I. aggregata*. Further work to investigate pollen fertility following exchange in both species and the patterns of gene flow in these populations would be necessary to fully determine the level of interspecific gene flow and potential for introgressive hybridization.

Our work shows that the narrow endemic *I. ramosa* is an outcrossing-dependent species serviced by a generalist pollinator and maintained via distinct patterns of floral form. The rarity of *I. ramosa* is thus likely a result of a chance interspecific hybridization with *I. aggregata* which gave rise to a species with different floral form. This difference in form gave rise to a partial pollinator shift utilizing a generalist pollinator with cross-pollination controlled by mechanical differences in flower structure with sympatric *I. aggregata*. Given the current stability of the known populations and their reliance upon a common generalist pollinator it does not appear that this rare species faces any threats associated with reproduction and breeding system.

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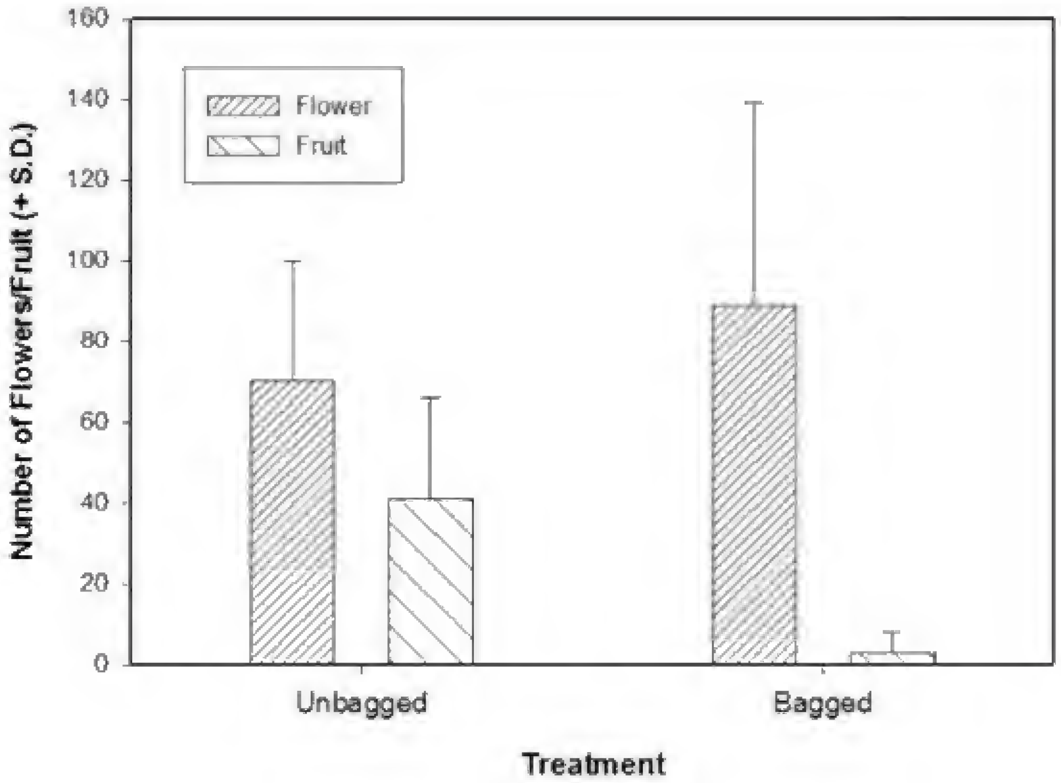

Figure 1. Average (+ S.D.) number of flowers and fruits produced in outcrossing and pollinator exclusion treatments in *Ipomopsis ramosa*.

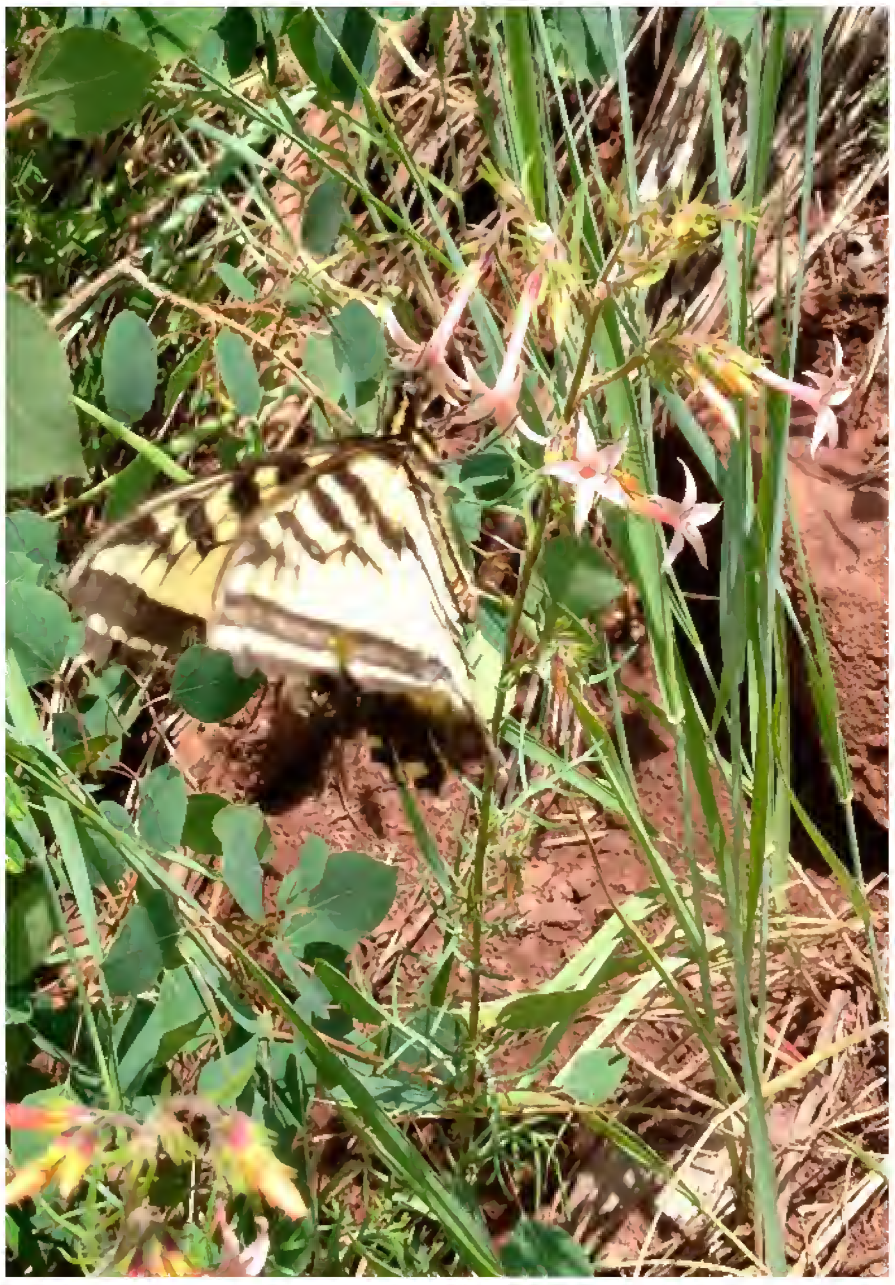

Figure 2. *Papilio rutulus* visiting flowers of *Ipomopis ramosa* in Roaring Forks Canyon.

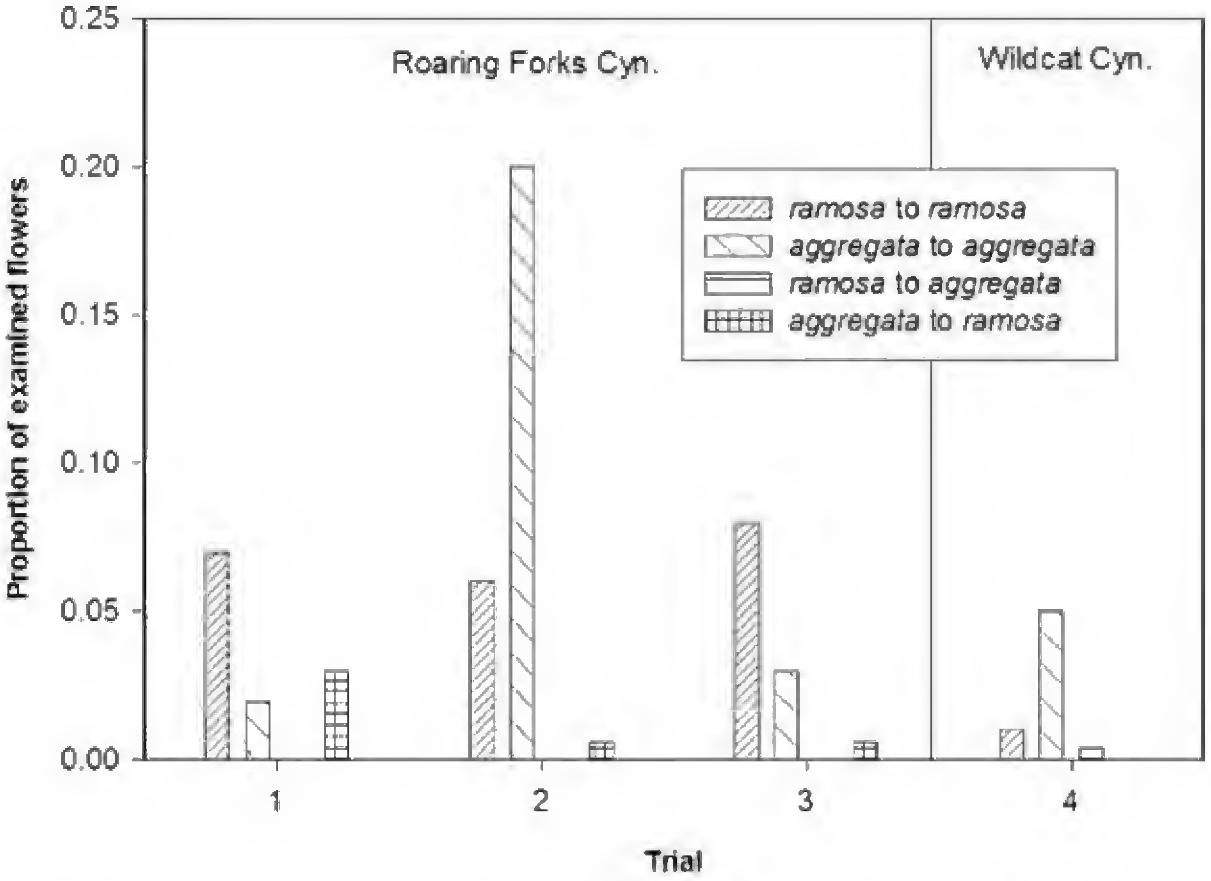

Figure 3. Proportion of examined flowers expressing transported dye particles in four trials across two areas of *Ipomopsis ramosa* occurrence.

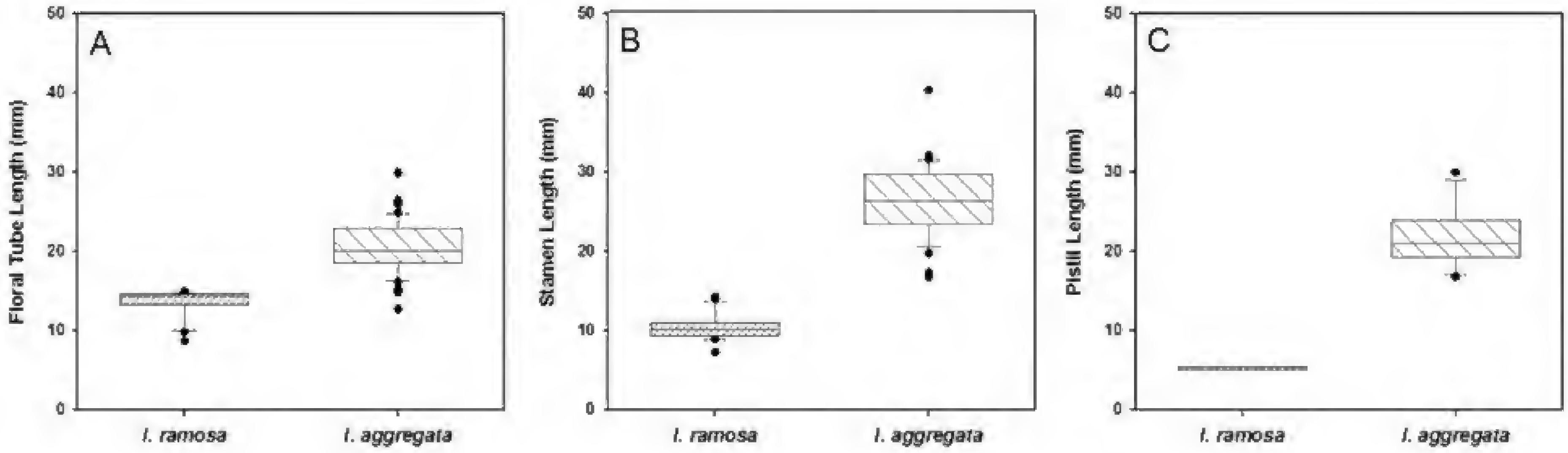

Figure 4. Comparison of floral morphology between *Ipomopsis ramosa* and *Ipomopsis aggregata* growing sympatrically in Roaring Forks Canyon. A. Floral tube length. B. Stamen length. C. Pistil length.

A New Senegalia (*S. seigleri*, Fabaceae: Mimosoideae) from Bahia, Brazil

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ABSTRACT

Senegalia seigleri Ebinger (Fabaceae, Mimosoideae) is described from Bahia, Brazil. The new species is illustrated and compared with its probable nearest relatives. Published on-line www.phytologia.org *Phytologia 99(2): 126-129 (May 9, 2017).* ISSN 030319430.

KEY WORDS: *Senegalia*, *Acacia*, Mimosoideae, Fabaceae, Brazil, Bahia, IUCN Red List

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Senegalia comprises approximately 102 taxa in the Neotropics (Barros & Morim 2014), 68 in Africa, 45 in Asia, and two in Australia (Maslin et al. 2003a, 2003b; Maslin 2015); of these, eight species occur in two or more areas. Both the Old and New World members of the genus are trees, shrubs, or lianas, armed with prickles, and lacking paired stipular spines. The prickles usually are scattered but in some species are grouped in twos or threes, usually at or near to the nodes; they also occasionally occur in lines and are rarely fused together into lines. Prickles can also occur on the petiole and rachis. Leaves are consistently bipinnately compound with 1 to 50+ pairs of pinnae, the pinnae having 1 to 80+ pairs of leaflets. The usually small leaflets are mostly linear to oblong, not exceeding 10 mm in length, but a few species have leaflets that are lanceolate to oblanceolate and may occasionally exceed 100 mm in length. The petiole and rachis have sessile or stipitate glands in variable positions, though sometimes the glands become specialized and of variable shape with the structure and shape being consistent within a species and of diagnostic importance. The mostly 5-merous (rarely 4-merous) flowers are campanulate, actinomorphic, synsepalous, sympetalous, with numerous stamens (usually 40 to 100), the filaments are mostly not fused and are attached to a more or less tubular or campanulate nectar disc located on the receptacle of the flower, surrounding the usually stipitate ovary. Inflorescences are globose heads or cylindrical spikes occurring solitary or in small clusters in the leaf axils, or grouped into complex axillary or terminal pseudoracemes or pseudopanicles. The legumes are oblong or broadly linear fruits that mostly separate into two valves at maturity. A few species have tardily dehiscent or indehiscent fruits, and some fruits rarely separate into one-seeded loments. The 6 to 20 uniseriate seeds are mostly strongly flattened and have a well-developed pleurogram.

During the course of ongoing work on *Senegalia,* an undescribed species occuring in the state of Bahia in northeastern Brazil was noted from herbarium material. Later, I observed that this material had been examined by Lewis (1987) who declared it to be a new species, but did not name or describe the material. This taxon is clearly distinct and is herein proposed as a new species.

Senegalia seigleri Ebinger, sp. nov. TYPE. Brazil. Bahia: Mun. de Una, Estrada Ilhéus-Una, ± 35 km. de Olivença, ca 15°16'S, 39°04'W, 30 m, (fl.) 2 Dec 1981, *G.P. Lewis & A.M. de Carvalho 731* (holotype: NY). Figure 1.

Diagnosis. *Senegalia seigleri* Ebinger differs from other *Senegalia* by the stamen filaments being distinct above but fused to an elongated tubular nectary that surrounds most of the sessile ovary for a length of about 1.2 mm; the two sessile, oval petiolar glands scattered along the petiole; the smaller but similar rachis glands usually between the uppermost 1 to 2 pinna pairs; the pinnae 4 to 6 pairs/leaf; the leaflets 19 to 36 pairs/pinna with the midvein located submarginal at the base, becoming subcentral at the apex; and the inflorescence a densely 15- to 35-flowered globose head in clusters of 2 to 6 in some leaf axils.

Scrambling to erect **shrub** to 3 m tall; bark not seen; twigs dark purple to purplish brown, not flexuous, terete to slightly ridged, glabrous; short shoots absent; prickles light purplish brown, the apex mostly darker, flattened, recurved, woody, 1-2 x 1-3 mm at the base, glabrous, persistent, common along the twig, petiole and rachis. **Leaves** alternate, 40-70 mm long; stipules not seen; petiole adaxially grooved, 20-30 mm long, glabrous to lightly pubescent; petiolar glands 2, scattered along the petiole with one usually near the lowermost pinna pair, sessile, oval, 0.6-0.9 mm across, apex cup-shaped, glabrous; rachis adaxially grooved, 25-55 mm long, lightly puberulent, an oval gland 0.3-0.7 mm across usually between the uppermost 1 to 2 pinna pairs, apex depressed, glabrous; pinnae 4 to 6 pairs/leaf, 25-60 mm long, 5-10 mm between pinna pairs; paraphyllidia 0.1-0.3 mm long, commonly absent; petiolule 1.1-1.8 mm long; leaflets 19 to 36 pairs/pinna, opposite, 0.7-1.2 mm between leaflet pairs, linear, 4.1-8.2 x 0.9-1.8 mm, glabrous beneath, lateral veins usually obvious, base oblique, truncate on one side, margins not ciliate, apex broadly acute, midvein submarginal at the base, becoming subcentral at the leaflet apex. **Inflorescence** a densely 15- to 35-flowered globose head 15-19 mm across, in clusters of 2 to 6 in the leaf axis; peduncles 8-10 x 0.5-0.8 mm thick, puberulent; receptacle not enlarged; involucre one small bract located on the upper half of the peduncle, early deciduous; floral bracts spatulate, 0.3-0.7 mm long, puberulent, early deciduous. **Flowers** sessile, white; calyx 5-lobed, 3.5-4.5 mm long, appressed puberulent; corolla 5-lobed, 4.2-5.1 mm long, usually glabrous, lobes one-quarter the length of the corolla; stamens 60 to 90, stamen filaments 7.5-9.1 mm long, distinct above, fused below to a tubular nectar disk to 1.2 mm long that surrounds most of the sessile ovary; anther glands absent; ovary sessile, glabrous. **Legumes** not seen. **Seeds** not seen.

Distribution and ecology: *Senegalia seigleri* was collected from a disturbed roadside site, near sea level in southern coastal Bahia, Brazil.

IUCN Red List Status: *Senegalia seigleri* appears to be genuinely rare. Following IUCN (2016) guidelines, a status of VU D2 is proposed, because the new species is known to exist at less than five locations, and only in the state of Bahia, Brazil.

Phenology: *Senegalia seigleri* was collected in flower in February.

Etymology: *Senegalia seigleri* is named for David S. Seigler (1940-), an authority on mimosoid legumes, especially *Acacia* in the broad sense, and curator of the University of Illinois Herbarium (ILL), University of Illinois, Urbana, Illinois, USA.

Discussion: During the examination of numerous specimens of South American *Senegalia* species over the past 32 years I have found 29 species that occur in the state of Bahia in northeastern Brazil. These species include: *S. amazonica* (Benth.) Seigler & Ebinger, *S. aristeguietana* (L. Cárdenas) Seigler & Ebinger, *S. bahiensis* (Benth.) Seigler & Ebinger, *S. fiebrigii* (Hassler) Seigler & Ebinger, *S. giganticarpa* (G. P. Lewis) Seigler & Ebinger, *S. globosa* (A. Bocage & Miotto) de Queiroz, *S. grandisiliqua* (Vellozo) Seigler & Ebinger, *S. grandistipula* (Benth.) Seigler & Ebinger, *S. harleyi* Seigler, Ebinger & Ribeiro, *S. hoehnei* Seigler, M. P. Morim, M. J. E. Barros & Ebinger, *S. irwinii* Seigler, Ebinger & Ribeiro, *S. kallunkiae* (J. W. Grimes & Barneby) Seigler & Ebinger, *S. lacerans* (Benth.) Seigler & Ebinger, *S. langsdorffii* (Benth.) Seigler & Ebinger, *S. lasiophylla* (Benth.) Seigler & Ebinger, *S. loretensis* (J. F. Macbride) Seigler & Ebinger, *S. martii* (Benth.) Seigler & Ebinger, *S. noblickii* Seigler & Ebinger, *S. olivensana* (G. P. Lewis) Seigler & Ebinger, *S. paganuccii* Seigler, Ebinger & Ribeiro, *S. paraensis* (Ducke) Seigler & Ebinger, *S. parviceps* (Speg.) Seigler & Ebinger, *S. piauhiensis* (Benth.) Seigler & Ebinger, *S. polyphylla* (DC.) Britton & Rose, *S. riparia* (Kunth) Britton & Rose, *S. rostrata* (Willd.) Seigler & Ebinger, *S. seigleri* Ebinger, *S. tenuifolia* (L.) Britton & Rose, and *S. tubulifera* (Benth.) Seigler & Ebinger. Of the species listed above, some are common species that occur throughout much of South America and sometimes extend into Central America (*S. loretensis, S. parviceps, S. polyphylla, S. riparia,* *S. tenuifolia,* and *S. tubulifera*). Others are rare, and in some cases endemic to Bahia (*S. kallunkiae, S. lasiophylla, S. olivensana,* and *S. seigleri*).

The presence of an elongated tubular nectariferous disk to 1.2 mm in length is rarely encountered in the *Senegalia.* Rico-Arce (2007, p. 21) mentions that some species of *Acacia* s. l. "have stamens joined into small groups or into a short tube," but only lists one example, *Acacia scleroxyla* Tussac [= *Senegalia skleroxyla* = *Parasenegalia skleroxyla* (Tussac) Seigler & Ebinger]. I have rarely encountered this character in individual specimens, but it is not consistent within any *Senegalia* species. Also, I have not seen enough material to determine if this character is consistent with the species *S. seigleri.* Because the existing specimen lacks fruits and seeds, and has only a few flowers in poor quality inflorescences, it is not possible to place *S. seigleri,* without some doubt, into a particular species group. However, the presence of two oval, sessile petiolar glands suggests a relationship with species similar to *S. riparia* and is tentatively placed with this species. All species that I have encountered in the state of Bahia that have two (or more) petiolar glands are keyed below.

Key to the species of *Senegalia* from Bahia with petioles that have two (or more) glands.

1. Inflorescence a long or short cylindrical spike.
  2. Leaflets 4-6 x 0.8-1.4 mm, 25 to 40 pairs/pinna .... *S. paganuccii*
  2. Leaflets 12-30 x 4-10 mm, 7 to 25 pairs/pinna .... *S. grandistipula*
1. Inflorescence a globose head.
  3. Petiolar and rachis glands columnar or funnel-shaped with a definite stalk.
    4. Leaflets 6-12 x 1.1-1.8 mm wide .... *S. irwinii*
    4. Leaflet less than 5 mm long and 1 mm wide.
      5. Rachis glands funnel-shaped, present between most pinna pairs; globose heads 7-11 mm across .... *S. grandisiliqua*
      5. Rachis glands mostly columnar, present between the uppermost 1 to 10 pinna pairs; globose heads 12-17 mm across .... *S. hoehnei*
  3. Petiolar and rachis glands sessile, not columnar or funnel-shaped.
    6. Leaflets 4-8 mm wide, 6 to 11 pairs/pinna .... *S. olivensana*
    6. Leaflets less than 2 mm wide, 18 or more pairs/pinna.
      7. Twigs, petiole and rachis densely pubescent with erect hairs to 0.6 mm long; petiolar glands 1 to 3 scattered along the petiole .... *S. harleyi*
      7. Twigs, petiole and rachis mostly glabrous or nearly so; petiolar glands 1 or 2.
        8. Petiole gland mostly solitary, elliptical to oblong, 1.9-7.2 mm long, with raised margins; globose heads 9-13 mm across .... *S. fiebrigii*
        8. Petiolar glands usually 2, oval to orbicular, less than 2.5 mm long; globose heads 13-20 mm across.
          9. Leaflet midvein central to subcentral nearly throughout; calyx 1.5-2.9 mm long .... *S. riparia*
          9. Leaflet midvein submarginal at base, becoming subcentral at leaflet apex; calyx 3.5-4.5 mm long .... *S. seigleri*

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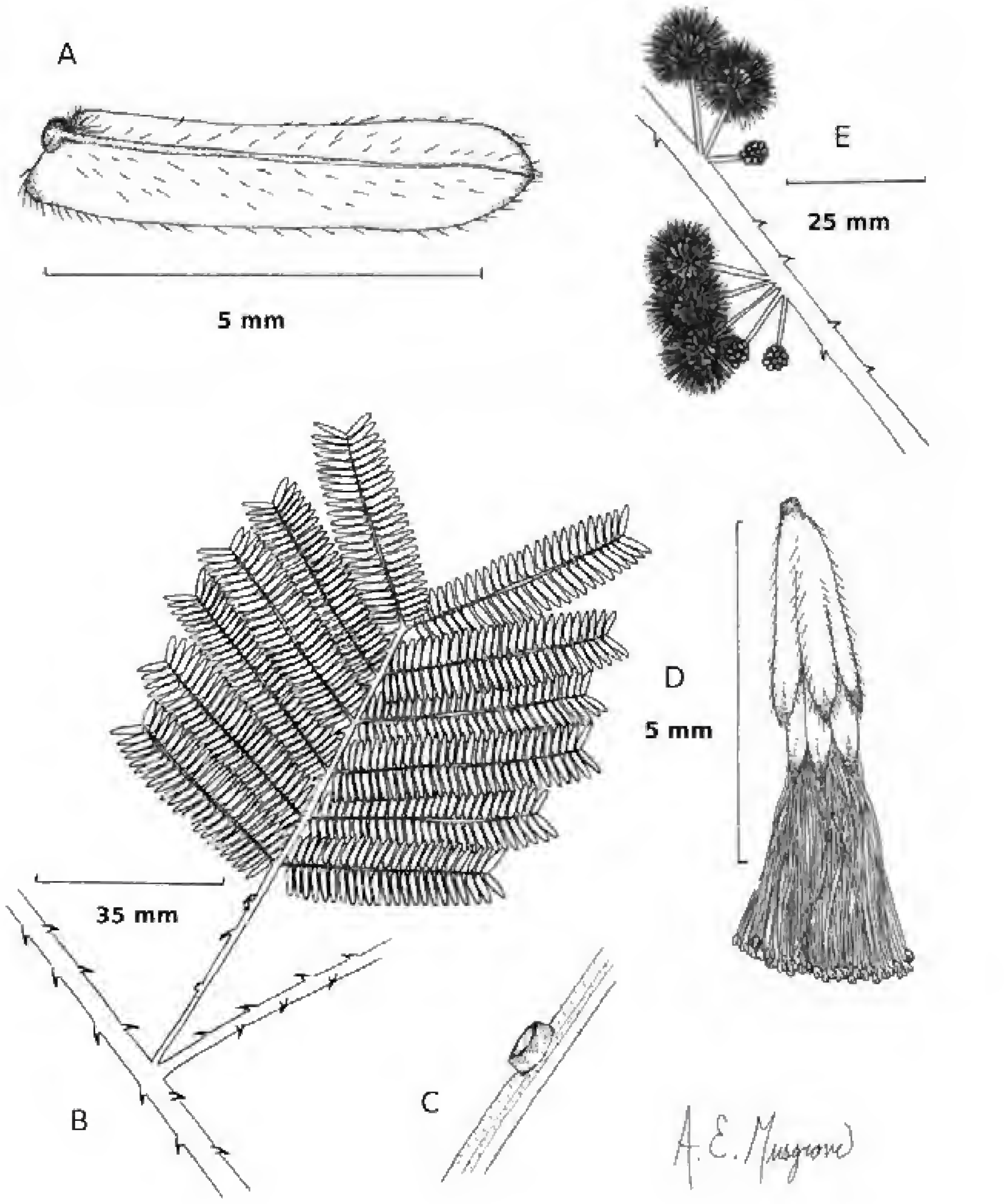

Figure 1. A. Leaflet, abaxial view; B. Leaf and portion of stem; C. Petiolar gland; D. Flower; E. portion of pseudoinflorescence

Geographic variation in volatile leaf oils (terpenes) in natural populations of *Helianthus annuus* (Asteraceae, Sunflowers)

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ABSTRACT

The composition of the steam volatile essential oils in leaves from 23 populations of *Helianthus annuus*, ranging from eastern Oklahoma to coastal southern California, were analyzed by GCMS. The oil compositions of populations from the southern high plains (KS, OK, TX) were uniform and dominated by α-pinene (50.5%), bornyl acetate (12.2), camphene (8.7), β-pinene (5.1), limonene (4.8) and sabinene (3.5). The oil composition from the quite distant San Diego was similar to the Plains populations: α-pinene (47.5%), sabinene (12.5), limonene (5.6), β-pinene (4.6), bornyl acetate (3.1) and camphene (2.7). Populations divergent from the Plains composition were Preston, ID: α-pinene (31.4%), bornyl acetate (21.0), limonene (7.2), camphene (6.7), and β-pinene (5.8); Redmond, OR: α-pinene (28.3%), bornyl acetate (16.8), germacrene D (8.2), limonene (7.2) and camphene (7.2); Eagle Nest, NM: α-pinene (27.3%), bornyl acetate (16.3), germacrene D (15.6), and β-pinene(5.3); and Camp Verde, AZ: germacrene D (19.1%), α-pinene (17.4), limonene (10.0) and β-phellandrene (6.7%). A population at Woodward, OK appeared to be an escaped commercial cultivar. Its oil was quite different and dominated by: β-pinene(27.3%) and germacrene D (25.4). Published on-line www.phytologia.org *Phytologia 99(2): 130-138 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: *Helianthus annuus,* Sunflower, geographic variation in volatile essential oil yields, monoterpenes, sesquiterpenes, di-terpenes.

Annual sunflower (*Helianthus annuus* L.) is an important crop ranked as the second largest hybrid crop (only behind maize (*Zea mays* L.) with a global crop value of $20 billion (Seiler, Qi and Marek, 2017).

In spite of the enormous amount of research on sesquiterpene lactones in *Helianthus annuus* (a search of Google Scholar revealed 1,350 papers), we have found only two papers on the composition of volatile leaf essential oil. Ceccarini et al. (2004) reported on the composition of the steam volatile leaf and seed head essential oils of two *H. annuus* cultivars growing in Italy: 'Carlos' and 'Florom 350'. They reported the leaf oils of the two cultivars to be very similar with the major components being: α-pinene (28.2, 28.9%), sabinene (23.5, 23.2), limonene (11.1, 12.3), (iso) bornyl acetate (8.0, 7.9) and germacrene D (8.2, 8.8). From our survey (below) it seems likely that Ceccarini et al. found bornyl acetate rather than iso-bornyl acetate as they elute at about the same retention times and their MS differ by only mass 80 > 82 in bornyl acetate and 80 < 82 in iso-bornyl acetate. All our samples had mass 80 > 82, indicating the occurrence of bornyl acetate.

The second paper on essential oils of *H. annuus* (Ogunwande et al. 2010), examined the cultivated sunflower in Nigeria and reported the essential oil was dominated by α-pinene (16.0%), sabinene (9.4), germacrene D (14.4), and 14-hydroxy-α-muurolene (9.0).

Spring and Schilling (1989) published a thorough chemosystematic investigation of annual species of *H. annuus*, but their work was based on sesquiterpene lactones. There does not appear to be any information on geographic variation in the leaf essential (terpenes) oil of *H. annuus*. The purpose of this report is to present detailed analyses on the composition of steam volatile leaf terpenoids of *H. annuus* and on geographic variation in these oils. This is continuation of our research on sunflowers (Adams and TeBeest 2016, Adams et al. 2016, Adams et al. 2017).

MATERIALS AND METHODS

Population locations - see Adams et al. 2017.

The lowest growing, non-yellowed, 10 mature leaves were collected at stage R 5.1-5.3 (see Adams et al. 2017 for photos of sunflower growth stages) when the first flower head opened with mature rays. The leaves were air dried in paper bags at room temperature for transporting from the field, then kept frozen until analyzed. No doubt this resulted in some losses of the most volatile components (cf. α-pinene, etc.), but under the circumstances, this could not be avoided.

Isolation of Oils - Ten (10) leaves (200 g) were steam distilled for 2 h using a circulatory Clevenger-type apparatus (Adams 1991). The oil samples were concentrated (ether trap removed) with nitrogen and the samples stored at -20°C until analyzed. The extracted leaves were oven dried (100°C, 48 h) for determination of oil yields.

Chemical Analyses - The oils were analyzed on a HP5971 MSD mass spectrometer, scan time 1 sec., directly coupled to a HP 5890 gas chromatograph, using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column (see 5 for operating details). Identifications were made by library searches of our volatile oil library (Adams, 2007), using the HP Chemstation library search routines, coupled with retention time data of authentic reference compounds. Quantitation was by FID on an HP 5890 gas chromatograph using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column using the HP Chemstation software.

Data Analysis - Terpenoids (as per cent total oil) were coded and compared among the species by the Gower metric (1971). Principal coordinate analysis was performed by factoring the associational matrix using the formulation of Gower (1966) and Veldman (1967).

RESULTS

Compositions of the steam volatile essential oils from leaves in several populations of *Helianthus annuus,* ranging from eastern Oklahoma to coastal southern California are given in Table 1. The compositions of populations from the southern high plains (Plains, Table 1, =KS, OK, TX) were uniform and dominated by α-pinene (50.5%), bornyl acetate (12.2), camphene (8.7), β-pinene (5.1), limonene (4.8) and sabinene (3.5). The quite distant San Diego population (SanD, table 1) had a composition similar to Plains populations: α-pinene (47.5%), sabinene (12.5), limonene (5.6), β-pinene (4.6), bornyl acetate (3.1) and camphene (2.7). Divergent populations from the Plains composition were Preston, ID (Pres ID, Table 1): α-pinene (31.4%), bornyl acetate (21.0), limonene (7.2), camphene (6.7) and β-pinene(5.8); Redmond, OR (Red OR, Table 1): α-pinene (28.3%), bornyl acetate (16.8), germacrene D (8.2), limonene (7.2) and camphene (7.2); Eagle Nest, NM (Eag NM, Table 1): α-pinene (27.3%), bornyl acetate (16.3), germacrene D (15.6), and β-pinene(5.3); and Camp Verde, AZ (Ariz, Table 1): germacrene D (19.1%), α-pinene (17.4), limonene (10.0) and β-phellandrene (6.7%). A population at Woodward, OK appeared to be an escaped commercial cultivar. The oil was quite different (WO, Woodw, Table 1) and was dominated by: β-pinene (27.3%) and germacrene D (25.4).

Fifteen (15) of the major terpenoids (boldface, Table 1) were utilized for computing similarities among populations (Gower, 1971). Factoring the similarity matrix resulted in five eigenroots before they began to asymptote. The five eigenroots accounted for 24.3, 15.4, 10.3, 7.5 and 7.1% of the variation among the populations. Principle Coordinates (PCO) of the similarity matrix revealed the major group as the Plains populations (Fig. 1) with the Woodward, OK (WO) population ordinated on axis 2. The plants in the Woodward population had very large, glabrous (no pubescence) leaves and larger seed heads than other populations. It appears that these are likely hybrids with commercial sunflowers. As noted above (and in Table 1), their essential oil is quite different from other *H. annuus* sampled. That is clearly seen in the PCO ordination (Fig. 1). The third axis serves to separate the more western populations from the Plains populations (Fig. 1).

Removing the Woodward, OK (WO) population and reanalyzing the terpenes resulted in five eigenroots that accounted for 27.6, 11.3, 8.6, 8.1, and 6.4% of the variance among the populations. Ordination (Fig. 2) shows a pattern similar to the previous pattern (Fig. 1), with the divergence western populations better resolved from the Plains cluster. Interestingly the San Diego populations (small leaves, SS, and large leaves SL) were near or within the Plains cluster (Fig. 2).

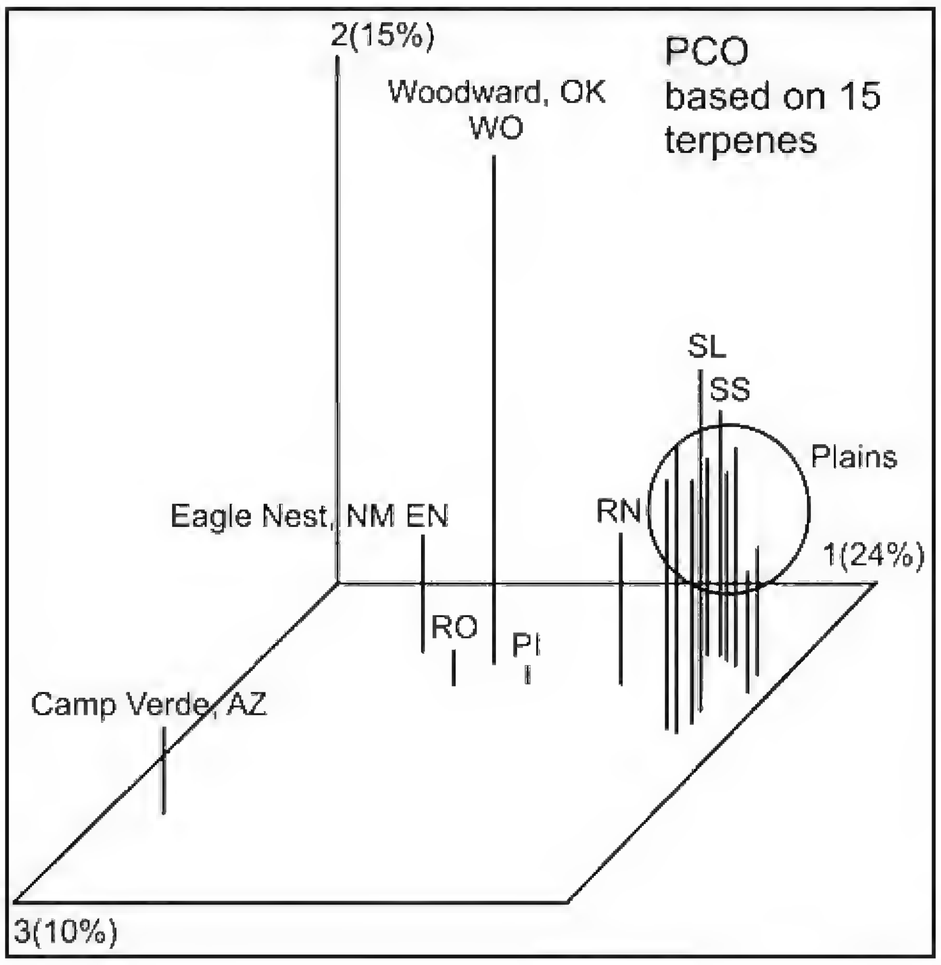

Figure 1. PCO based on 15 terpenes with Woodward (WO) included.

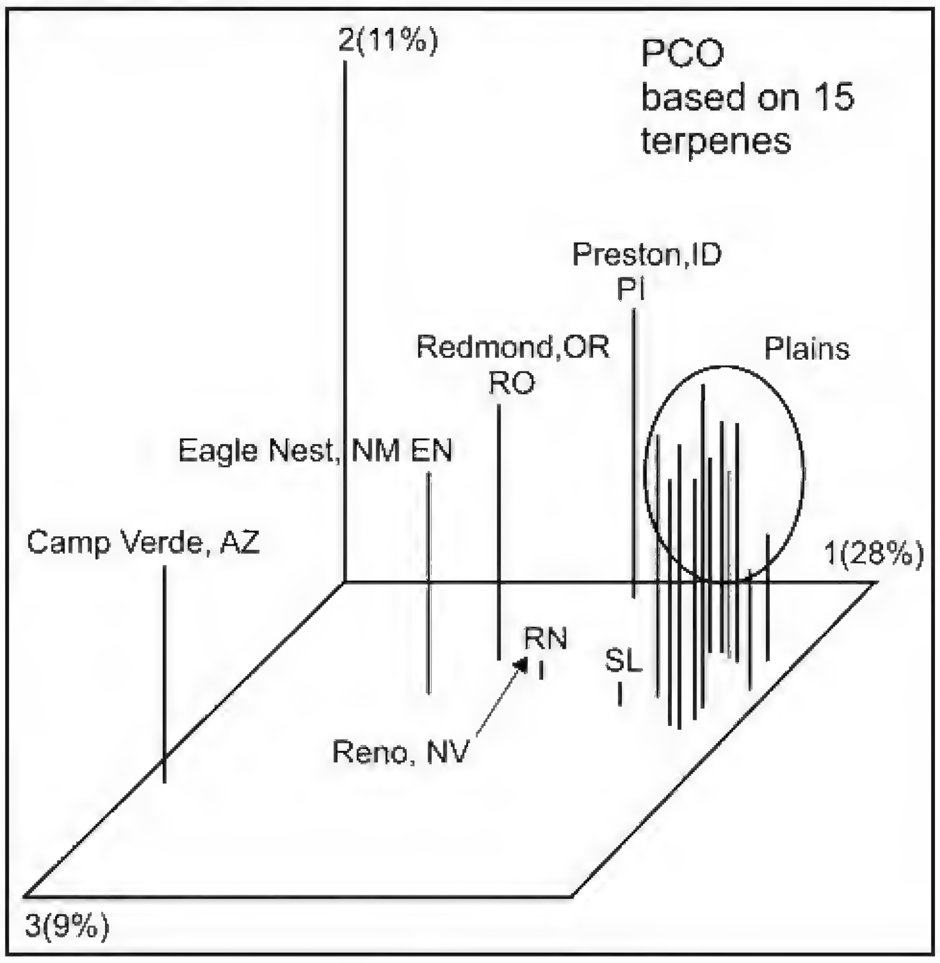

Figure 2. PCO based on 15 terpenes without the Woodward population.

Contouring the clustering of the populations clearly shows the geographic variation pattern (Fig. 3. The populations with the most similar volatile leaf oil compositions are those in the Plains group: KS, OK and ST (Sonora, TX, but grown from seed in the Texas Panhandle at Oslo, TX). Also closely joining the cluster are Texas Panhandle, south Plains and Central Texas (MC) populations (Fig. 3). The clustering of the disjunct sunflowers from San Diego is an anomaly. This kind of disjunct clustering is also seen for the Redmond, OR (RO) and Brigham City, UT (BU) populations, to some extent. Just as depicted in the PCO (Figs. 1, 2), Camp Verde, AZ (AZ, Fig. 3) is the last population to enter the cluster at a similarity of 0.68 (Fig. 3).

The San Diego populations might owe their origin to historical dispersal by settlers moving westward from Kansas on the California trail, who accidentally (or on purpose) carried seed from the Prairies to California. Or it may be that Native Americans dispersed the Plains seed into the western United States.

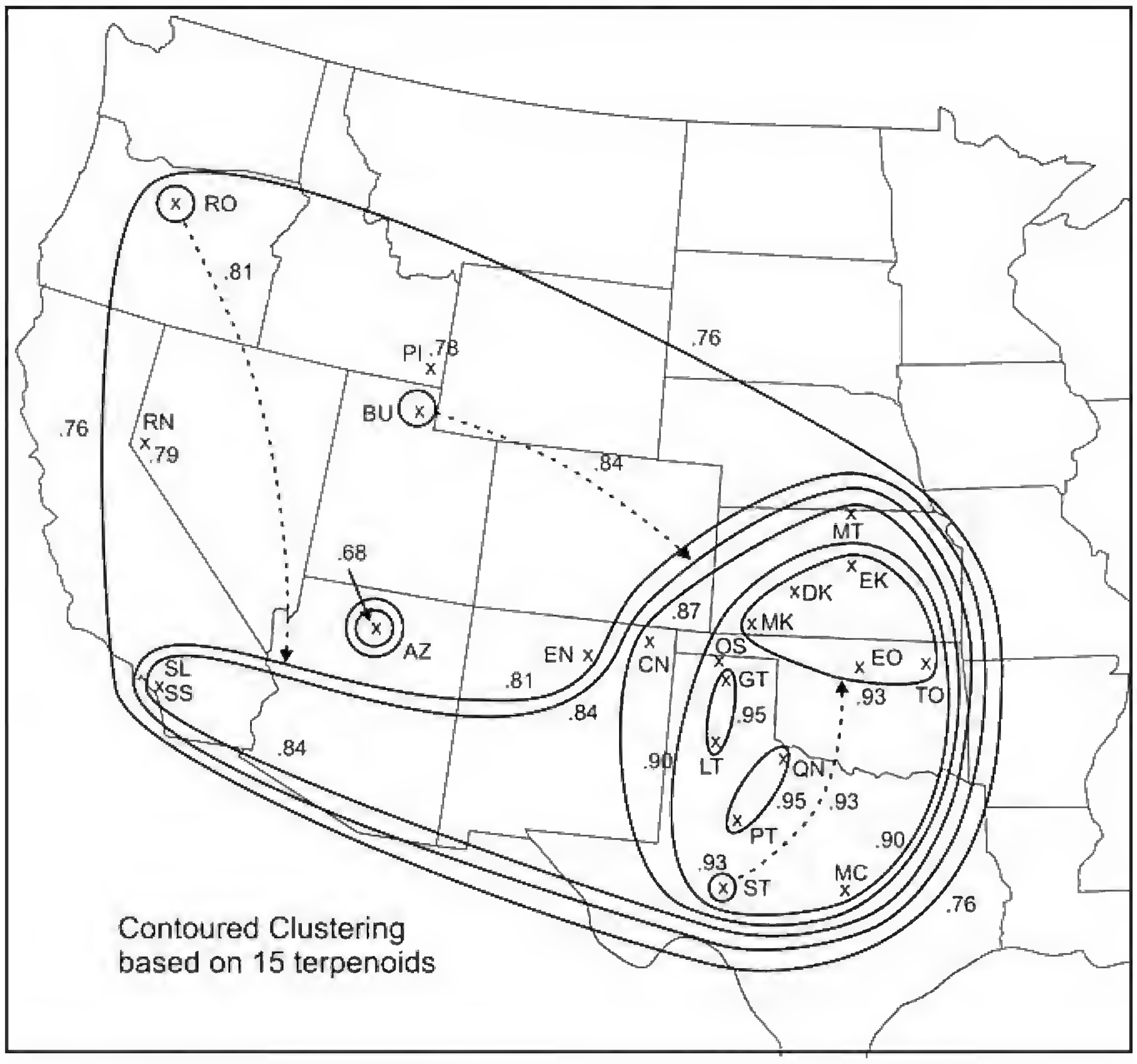

Figure 3. Contoured clustering of populations utilizing 15 major terpenes.

The yields of essential oils were computed as % yield and as g oil/ g of 10 air dried steam distilled leaves. The Montrose, KS (MT) population had the highest % yield of total essential oil (3.03%, Table 2, Fig. 4), followed by Capulin, NM (CM, 1.85%), Gruver, TX (GT, 1.47%), and Lake Tanglewood, TX (LT, 1.21%). The range of variation in % oil was quite extensive, from 3.03% (Montrose, KS) to 0.22% (Camp Verde, AZ).

The sunflowers growing in a prairie grassland at Oslo, TX (OS) population (which is only 15 miles from Gruver, TX) interestingly had a much lower % oil yield (0.80%) than plants growing on a roadside Gruver (1.21%). This may be due to an environmental influence on % oil yields rather than genetic differences. The sunflowers at Gruver were extensively attacked and eaten by grasshoppers and other insects. This may have triggered a defense mechanism to increase terpene (defense chemicals) synthesis. The large yield in the Montrose population was unexpected, but it should be noted that seeds from Montrose, KS were grown at Oslo, TX, from which leaves were collected. So, one can not be sure that the data represents what the MT would have produced *in situ*.

A different pattern of geographic variation exists in total oil yields (g oil/ g DW of 10 distilled leaves). Again, the largest yield was in the Montrose population (MT, 0.310 g, Table 2, Fig. 5), followed by Lake Tanglewood (LT, 0.225g), Gruver (GT, 0.223g), and Enid (EO, 0.206g). The Enid population was not very high in % oil yield (0.8%), but the plants were very large, resulting in a high g oil /10 leaves (0.206g).

The variation among populations in g oil/ g 10 leaves is greater than variation in % oil yields (Fig. 5, vs. Fig. 4). This is reasonable, as g oil/ g 10 leaves is greatly affected by the biomass of the plants, which is subject to microhabitat edaphic factors. Montrose, Lake Tanglewood, and Gruver were high in both % oil yields and g oil/ g DW 10 leaves (Table 2, Figs. 4, 5).

The correlation between % oil yields and % HC yields was low 0.339, explaining only 11.5% of the variation among populations. The correlation between g/g 10 leaves yields of essential oil and HC g/g 10 lvs was 0.675. This correlation accounts for 45.6% of the variation among populations. It may be that that the yields on a g/ g basis are highly influenced by environmental factors that are local to the population level, whereas, % yields are less influenced by environmental factors. I (RPA) have found that the yield of HC from greenhouse grown plants is only about 40% as much as from plants grown outside in the natural environment.

Clearly, more research is needed to determine the environmental versus genetic factors in the production of essential oils in *H. annuus*.

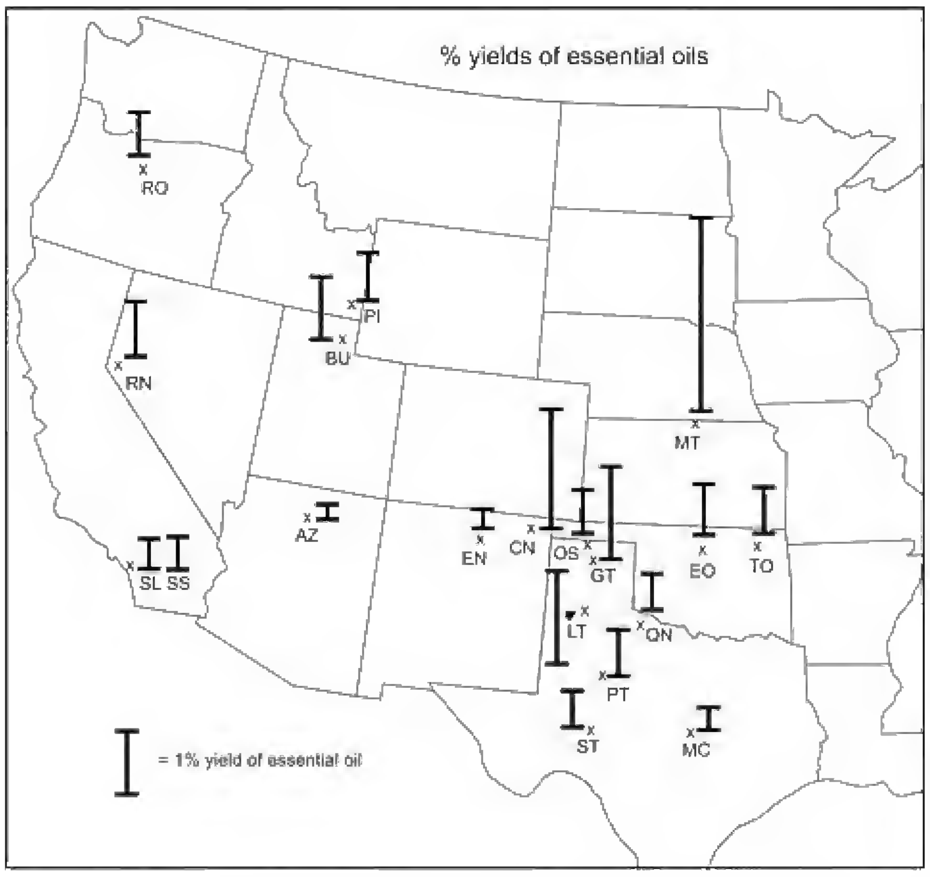

Figure 4. Plot of % oil yields. Note scale in lower left.

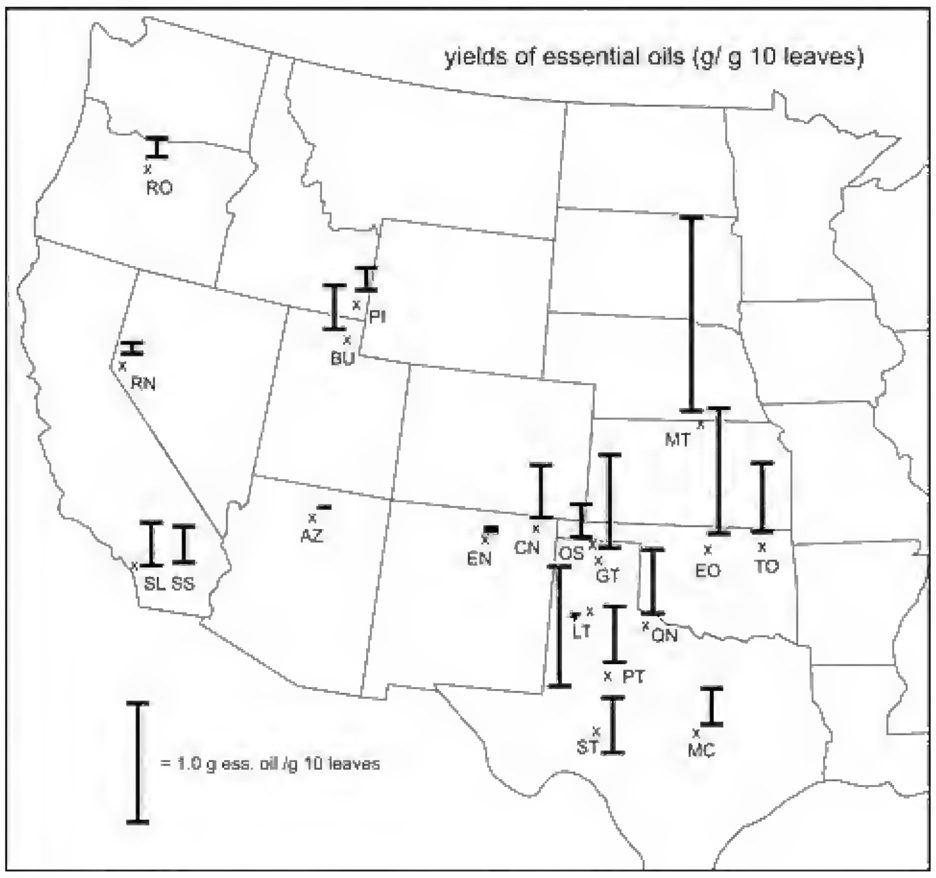
yields of essential oils (g/ g 10 leaves)
RO
PI
BU
RN
MT
AZ
EN
CN
OS
GT
EO
TO
SL SS
LT
QN
PT
ST
MC
= 1.0 g ess. oil /g 10 leaves

Figure 5. Plot of g oil/ g wt. of 10 dried leaves. Scale is in lower left.

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Table 1. Leaf essential oil compositions for *Helianthus annuus* populations. The 15 compounds in bold show large differences between samples and were used in PCO analysis. Plains = general pattern found in the Texas Panhandle, Kansas and western Oklahoma. Woodw = population of cultivated escaped sunflowers at Woodward, OK, Ariz = Camp Verde, AZ, SanD = San Diego.

KI	compound	Plains	SanD	Reno	Pres ID	Red OR	Eag NM	Ariz	Woodw
921	tricyclene	0.2	0.1	0.2	0.2	0.2	t	t	t
924	α-thujene	0.4	0.1	t	0.2	0.1	t	t	t
932	**α-pinene**	**50.2**	**47.5**	**37.3**	**31.4**	**28.3**	**27.3**	**17.4**	**6.8**
946	**camphene**	**8.7**	**2.7**	**4.5**	**6.7**	**7.2**	**3.5**	**0.9**	**2.2**
969	**sabinene**	**3.5**	**12.0**	**2.3**	**3.0**	**2.3**	**1.7**	**4.8**	**6.3**
974	**β-pinene**	**5.1**	**4.6**	**4.9**	**5.8**	**4.6**	**5.3**	**3.2**	**27.3**
988	myrcene	0.3	0.7	0.4	0.7	0.5	0.8	0.8	0.3
1005	(2E,4E)-heptadienal	t	-	-	t	-	-	-	0.1
1014	α-terpinene	t	-	-	t	-	t	-	t
1020	p-cymene	t	0.1	t	0.2	t	t	t	t
1024	**limonene**	**4.8**	**5.6**	**4.5**	**7.2**	**7.2**	**2.6**	**10.0**	**0.9**
1025	**β-phellandrene**	**t**	**3.8**	**3.0**	**5.0**	**4.6**	**1.8**	**6.7**	**0.6**
1036	benzene acetaldehyde	-	0.1	0.3	0.1	0.1	t	0.2	-
1044	(E)-β-ocimene	-	t	t	t	t	t	t	0.3
1054	γ-terpinene	0.1	0.1	t	0.3	0.1	0.2	0.1	0.1
1065	cis-sabinene hydrate	t	t	-	0.1	t	t	t	0.1
1086	terpinolene	-	0.1	t	0.2	0.1	0.3	t	t
1098	trans-sabinene hydrate	-	-	-	0.2	-	t	0.1	t
1099	α-pinene oxide	0.3	0.2	0.4	-	-	-	-	-
1105	43,109,137,152	0.5	0.5	1.4	0.4	0.1	0.4	-	-
1123	α-camphenal	0.3	0.3	0.5	0.2	-	t	-	t
1135	trans-pinocarveol	0.1	0.3	0.8	0.1	t	0.2	0.1	0.6
1137	cis-verbenol	0.1	-	-	0.1	-	-	-	-
1140	**trans-verbenol**	**1.0**	**1.0**	**1.9**	**0.6**	**0.3**	**0.7**	**0.6**	**0.2**
1160	pinocarvone	0.2	0.2	0.3	0.2	t	t	t	0.2
1165	borneol	0.4	t	0.4	0.3	0.1	3.3	t	7.5
1174	terpinen-4-ol	0.1	-	-	0.2	-	0.2	t	0.4
1179	p-cymen-8-ol	t	-	-	-	-	-	t	t
1186	α-terpineol	t	-	-	-	-	-	-	0.1
1195	myrtenal	0.2	0.1	0.2	0.1	-	t	-	0.1
1195	myrtenol	t	0.2	0.5	-	-	-	t	0.1
1204	verbenone	0.2	-	0.2	0.1	-	t	-	-
1212	55,83,135,154	-	0.1	-	-	-	-	-	0.3
1215	trans-carveol	-	t	0.2	-	-	-	-	-
1287	**bornyl acetate**	**12.2**	**3.1**	**9.7**	**21.0**	**16.8**	**16.3**	**4.2**	**5.5**
1298	trans-pinocarvyl acetate	0.2	0.2	0.5	0.3	0.3	0.3	t	-
1324	myrtenyl acetate	-	t	0.1	-	-	-	-	-
1356	eugenol	-	-	-	-	-	-	-	0.2
1374	α-copaene	-	-	-	-	-	t	t	0.1
1387	β-bourbonene	0.1	t	1.5	t	0.1	0.2	0.3	0.2
1387	β-cubebene	t	-	-	t	-	0.2	0.4	t
1389	β-elemene	t	-	-	-	-	t	0.1	0.2
1392	(Z)-jasmone	-	-	-	-	-	-	-	0.2
1417	**(E)-caryophyllene**	**0.2**	**0.2**	**0.3**	**0.1**	**0.5**	**1.0**	**1.0**	**2.7**
1430	β-copaene	-	t	0.2	-	-	-	t	0.1
1432	α-trans-bergamotene	0.1	t	0.2	0.1	-	t	t	-
1439	aromadendrene	-	-	0.2	-	-	-	-	-
1452	geranyl acetone	0.1	0.2	0.1	-	0.1	t	0.2	-
1452	α-humulene	0.1	t	t	0.3	0.3	0.6	0.5	0.6
1480	**germacrene D**	**2.8**	**2.6**	**0.5**	**1.9**	**8.2**	**15.6**	**19.1**	**25.4**
1489	β-selinene	0.1	-	-	0.2	-	0.2	-	-
1493	epi-cubebol	-	0.2	0.1	t	0.2	t	-	-
1500	bicyclogermacrene	-	-	-	-	-	-	-	0.9

KI	compound	Plains	SanD	Reno	Pres ID	Red OR	Eag NM	Ariz	Woodw
1513	γ-cadinene	-	-	-	t	-	t	0.2	t
1522	δ-cadinene	-	-	-	t	-	0.3	0.3	0.1
1559	**germacrene B**	**-**	**-**	**-**	**1.1**	**-**	**0.4**	**1.1**	**-**
1561	1-nor-bourbonene	-	-	-	-	-	-		0.3
1574	germacrene D-4-ol	0.2	-	-	0.1	-	1.5	1.1	-
1577	spathulenol	0.2	t	0.4	t	-	t		-
1582	caryophyllene oxide	0.2	0.1	0.4	0.2	-	0.3	0.2	1.0
1594	salvial-4(14)-en-1-one	-	0.1	0.2	-	-	-	-	-
1602	41,95,161,222	-	-	-	t	-	-	0.7	-
1608	humulene epoxide II	0.2	-	-	-	-	0.5	-	1.2
1618	junenol	t	-	-	-	-	-	-	-
1638	epi-α-cadinol	t	-	0.6	0.3	0.2	0.9	0.1	-
1649	β-eudesmol	0.3	-	0.4	0.5	0.5	0.6	-	-
1665	**intermediol**	**0.4**	**0.6**	**0.6**	t	**0.3**	**0.4**	**0.2**	**1.6**
1685	**germacra-4(15),5,10(14)-trien-1-al**	**0.3**	**0.5**	**2.3**	**0.3**	**0.6**	**0.8**	**1.8**	**0.2**
1780	ledene oxide II*	-	0.6	1.4	t	0.3	0.6	0.9	-
1840	43,68,123,278	0.5	0.4	0.8	0.4	0.8	0.4	1.1	-
1840	hexahydrofarnesyl acetone	-	-	-	-	-	-	-	0.1
1931	beyerene	0.1	-	-	-	-	-	t	-
2009	13-epi-manoyl oxide	t	-	-	t	-	t	0.1	-
2114	phytol isomer	-	-	-	-	-	t	0.3	0.4
2148	41,91,105,135,286	0.3	-	0.5	0.5	0.4	0.4	1.4	-
2192	p-methoxybenzoic acid, 2-isopropoxyphenyl ester, isomer	-	-	-	-	-	-	-	0.4
2205	41,91,105,286	t	t	0.3	0.2	0.2	0.2	0.6	-
2216	atis-16-ene* <5β,8α,9β,10α,12α->	**0.4**	**0.3**	**0.9**	**0.5**	**0.7**	**0.6**	**1.3**	**-**
2220	43,123,272,290	0.2	0.2	0.5	0.3	0.4	0.3	0.6	-
2235	43,232,272,290	t	0.1	0.3	0.3	0.3	0.3	0.6	-
2241	**105,135,257,288**	**0.5**	**0.1**	**0.9**	**0.7**	**1.0**	**0.5**	**1.4**	**-**
2253	41,257,91,286	-	0.1	0.2	0.4	0.2	0.3	0.9	-
2263	91,187,243,286	0.3	0.3	0.9	0.7	0.6	1.0	3.1	-

KI = linear Kovats Index on DB-5 column. Compositional values less than 0.1% are denoted as traces (t). Unidentified components less than 0.5% are not reported. *tentatively identified from NIST mass spectral database.

Table 2. Comparison of the yields volatile leaf oils and hydrocarbons (HC) for *H. annuus*, from natural populations. Correlation between % yields of essential oil and HC = 0.339; Correlation between g/g 10 leaves yields of essential oil and HC = 0.675.

popn id, sample ids	population sampled	volatile oil, % yield	HC, % yield	volatile oil g/10 lvs	HC yield g/10 lvs
PT P1 - P0	14935 Post, TX	0.81	4.36	0.095	0.481
QN Q1-Q0	14936 Quanah, TX	0.69	4.32	0.119	0.779
TO T1-T0	14942 Tulsa, OK	0.60	4.56	0.114	0.778
EO O1-OT	14943 Enid, OK	0.84	4.97	0.206	1.094
WO W1-W0	14944 Woodward, OK, (escaped cultivar)	0.25	2.62	0.047	0.644
ST S1-S0	14945 grown from seed, ex Sonora, TX, PI413168	0.70	5.19	0.089	0.744
OS O1-TO	14946 Oslo, TX,	0.80	5.95	0.082	0.508
LT: L1-L0	14947 Lake Tanglewood, TX	1.21	8.47	0.225	1.760
SS SA-SJ	14950 San Diego, CA, small leaves	0.55	4.59	0.035	0.335
SL SK-ST	14951 San Diego, CA, large leaves	0.47	4.68	0.056	0.54
GT1:G1-G0	14952 Gruver, TX	1.47	7.26	0.223	1.54
MC 1M-0M	14976 McLennan Co., TX	0.36	6.18	0.058	0.923
EN 1E-0E	14980 Eagle Nest, NM	0.31	2.62	0.013	0.143
CN 1C-0C	14981 Capulin, NM	1.85	5.29	0.098	0.232
MT MA-MC	14982 grown from seed ex Montrose, KS, PI 413033	3.03	4.91	0.310	0.518
AZ Z1-Z0	15021 Camp Verde, AZ	0.22	3.79	0.007	0.213
BU B1-B0	15022 Brigham City, UT	1.01	5.90	0.060	0.420
PI 1P-0P	15024 Preston, ID	0.80	6.30	0.028	0.338
RO R1-R0	15027 Redmond, OR	0.72	4.06	0.028	0.291
RN R1-R0	15029 Reno, NV	0.96	5.11	0.016	0.178

Notes on trifoliolate species of *Galactia* (Fabaceae) in Florida

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ABSTRACT

Galactia is an inordinately taxonomically difficult genus in the southeastern USA with wide variations in both circumscriptions and the application of names, despite the efforts of many botanists. This study focuses on the trifoliolate members within Florida and a key to their identification is provided. Illegitimate and misapplied names have persisted in usage, which has necessitated the description of two new species, *G. austrofloridensis* and *G. michauxii*. Additional discussion is provided for the trifoliolate species of *Galactia* in the southeastern USA. Specimens specifically matching the type specimen of *G. regularis* are not clearly evident in Florida. The lectotype of *G. volubilis* is accurate and must be followed, as there are numerous specimens matching its morphology (i.e. a retrorsely hirsute stem, well-spaced inflorescence nodes, twining habit, and glaucescent lanceolate-ovate leaflets). The delimitation of taxa within *Galactia* remains problematic. Published on-line www.phytologia.org *Phytologia 99(2): 139-185. (May 9, 2017)*. ISSN 030319430.

KEY WORDS: *Galactia*, Fabaceae, Florida, southeastern USA

Galactia P. Browne contains ~100–150 species (Rogers 1949; Nesom 2015) and is partly characterized by its caducous stipules, papilionaceous corolla, and 4-parted calyx (Adams 1972). The type of the genus is the West Indian *G. pendula* Pers. (Rose 1906; Burkart 1971). It is a taxonomically challenging genus in the southeastern USA and elsewhere. Anent the Bahama archipelago, Correll & Correll (1982: 644) wrote "This is one of the most frustrating genera in our flora [...] it is a rather hopeless task to make a workable key for their identification [...] Specimens "look different" from one another but they represent the zenith of frustration to the worker." Recent investigations have further explored relationships within *Galactia*, including a *matK* phylogeny that included a few specimens from the southeastern USA (de Queiroz et al. 2015: Fig. S3, pt. 2).

The few relatively clearly delimited species in the southeastern USA are *G. erecta, G. elliottii, G. mollis,* and *G. striata.* The remaining taxa of *Galactia* in the southeastern USA fall into the "*Galactia volubilis* group", as termed by Isely (1998), who noted that "members are not only seemingly introgressive, but recurrently and reticulately variable [...] features are variable within the taxa and none, singly or in correlation with others seem diagnostic. [...] Their confluent nature, however, results in the necessary use of key statements that overlap." A continuum of variation can be found for nearly any chosen morphological character.

Both species delimitation and the application of names have been profusely discordant for the "*G. volubilis* group" and few studies have cited specimens to document taxonomic concepts (Small 1933; Rogers 1949; Duncan 1979; Isely 1998; Ward & Hall 2004; Wunderlin & Hansen 2011; Nesom 2015). It is difficult to equate one author's sense of a taxon to another author's sense of a taxon without guesswork and affixing complicating qualifications such as "pro parte", "sensu", or "non" to particular authors. No matter the decided taxonomy, regardless of lumping, splitting, or attempting the middle ground, one cannot help but feel it is an unavoidably, convoluted mess. Infraspecific frameworks are so far generally unexplored partly because relationships are uncertain and potentially multiplicative.

Though dividing the "*G. volubilis* group" into cohesive entities is challenging, abundant morphological and ecological diversity with biogeographic patterns is present within the group. Many segregates can be chiseled away from the "*G. volubilis* group" (Isely 1998), such as *G. austrofloridensis* (sp. nov.), *G. floridana, G. michauxii* (sp. nov.), *G. microphylla, G. minor, G. pinetorum,* and *G. smallii.* At the core of the group lie the oldest available names, *G. regularis* and *G. volubilis*, which have only been considered part of *Galactia* since the late 1800s (Nuttall 1818; Torrey & Gray 1838; Vail 1895). The circumscriptions of these Linnaean names, the application of their type specimens, and the recognized defining characters have varied substantially.

All taxa of the "*G. volubilis* group" have relatively weak stems and rely on surrounding vegetation to achieve any significant vertical height. The perceived presence or absence of twining exhibited on specimens has been relied upon to sort many taxa into two primary groupings: a prostrate, non-twining group and a twining group (e.g. Vail 1895; Small 1933; Rogers 1949; Ward & Hall 2004; Nesom 2015). It is unclear how much twining varies on a plant or within a taxon, and if it can be characterized as entirely present or absent, especially based on herbarium specimens alone. For example, Rogers (1949: 90–91) stated "the growth habits of [*G. michauxii* (as *G.* "regularis")] do not seem to be of much taxonomic value" and described one plant which had both short erect stems and long decumbent branches with some tips twining. Specimens of the supposedly non-twining group that exhibit twining are not hard to find, e.g. *G. floridana* (*Lakela 25360*), *G. michauxii* (*Becker & Hattaway WC0311, Franck 1478*), and *G. smallii* (*Avery 2164*). Thus, by itself, twining does not appear to be a diagnostic character. Less twining might be expected in shorter, thicker, or more basal stems and in open areas in habitats such as flatwoods, sandhill, scrub, dunes, or pine rockland. More twining might be expected in thinner, distal stems and in areas with denser surrounding vegetation. Attentive fieldwork is needed to characterize aspects of plant habit, such as twining. Additional clarification might be gained from collections that include root structure and the base of the plant.

Another source of confusion may be the size of the flowers, whereby some studies specify the length of the corolla whilst others focus on the whole flower. It is as if these two measurements are being used interchangeably, but they could differ. It may be important when flower sizes exhibit a continuum among taxa. The mature flowers are subtended by two bracteoles that attach ~0.2–1 mm below the receptacular bulge. The receptacle could appear to be up to 0.8 mm long, from which the calyx arises. The calyx tube could be 2 mm long, enclosing the point of attachment of the corolla. Precisely measuring the corolla would require tearing away the calyx. The point of attachment of the corolla can certainly be approximated from the base of the calyx. Without magnification, it can be difficult to see the distinction between the bracts, receptacle, and base of the calyx, potentially causing variability in measurements. Here it is opted that the size of flower is a practical measurement that can be approximated from the base of the calyx to the tip of the keel (lower petal).

Molecular studies with extensive sampling may be useful to clarify or corroborate taxonomic treatments. Utilization of epitypes that very closely match type specimens in morphology and approximate locality may be desirable, especially if duplicates can be widely distributed to herbaria for additional study. Given the possibility of interbreeding among many taxa of *Galactia*, phylogenetic inferences from plastid DNA may be heavily influenced by biogeography and introgression (Rieseberg & Soltis 1991; Nevill et al. 2014; French et al. 2016), while the nucleus, comprising the bulk of a plant's unique genome, might be expected to reflect more of the morphology. Field studies, living plants, internal floral structures, and characters of the fruits and seeds have been rarely utilized (Duncan 1979) and might offer additional insight if explored more.

Additional discussion is provided below for the trifoliolate species of *Galactia* in the southeast USA. It is interpreted here that two putative taxa were previously given illegitimate or misapplied names, i.e. as *G. brachypoda*, misapplied (Nesom 2015), *G. glabella*, nom. illeg. (Duncan 1979), *G. grisebachii*, misapplied (Nesom 2015), or *G. parvifolia*, misapplied (Small 1933; Long & Lakela 1971; Isely 1998; Ward & Hall 2004). To address this problem, two species are described. A key to the Florida species is also provided that does not rely heavily on the degree of twining. Still, the key is merely an alternative to other systems and is not bereft of the same difficulties that plague the taxonomy of *Galactia*. The key may likely falter in attempting to categorize some specimens, an unfortunate pattern for *Galactia*. Specimens are cited below (Appendix 1) and figures presented (Appendix 2: Figs. 1–42) to document the taxonomic concepts. Specimens at FTG and USF were studied in person while all others were observed as digital images. All that can be said is that I have attempted a system most strongly derived from the close study of peninsular Florida specimens and that much more work is most importunately needed.

KEY TO SPECIES OF *GALACTIA* IN FLORIDA

1. Leaves 5-9 foliolate; corolla white [FL, s GA, s SC].. ***G. elliottii***

1. Leaves 3-foliolate; corolla white, pink, or reddish

  2. Plant erect, if twining, only at the distal tip of the stem; inflorescence sessile, subsessile, or pedunculate; petioles usually subequal to longer than the terminal leaflet at some or most mature nodes; corolla white to light pink

    3. Plant erect, not twining; most inflorescences sessile, occasionally with mature peduncles < 9 mm long [e TX to n FL to NC].. ***G. erecta***

    3. Plant erect and sometimes twining distally; most inflorescences pedunculate, mature peduncles > 6 mm long [FL and sw GA].. ***G. brachypoda***

  2. Plant prostrate, decumbent, clambering, or twining; inflorescence pedunculate, or if sessile then plant not erect; petioles usually subequal to shorter than the terminal leaflet, if petioles longer than terminal leaflet then plant not erect; corolla pink, purple to reddish

    4. Corolla and stamens reddish when dry or withered; inflorescence shoot-tip and immature fruits densely villous with spreading hairs [MS(?), AL to c FL to NC]...................................... ***G. mollis***

    4. Corollas and stamens light brown, whitish, to blue, pinkish, or purplish when dry or withered; inflorescence shoot-tip and immature fruits villous, strigose, or glabrate with hairs mostly ascending to appressed or not dense

5. Banner (upper petal) often with white stripes adaxially, the base yellow to greenish yellow; mature inflorescence often with more than 15 flowers, nodes numerous and congested throughout the upper half of the rachis; fruit 5.5–9 mm wide; leaflets often with prominent pale, straw-colored secondary venation abaxially and reticulate venation inconspicuous adaxially [south FL] .... ***G. striata***

5. Banner usually without white stripes or only the midvein white adaxially, the base mostly white; mature inflorescence usually with less than 15 (–25) flowers, nodes not congested or only congested in the upper third of the rachis; fruit < 6 mm wide; leaflets with secondary venation not prominent abaxially, or if prominent then somewhat reddish and reticulate venation conspicuous adaxially

  6. Stems villous, canescent, tomentose, or pilose (glabrate on older stems), hairs mostly spreading to oblique, not appressed; hairs often persistent on calyx and adaxially on leaves

    7. Mature leaflets with abaxial secondary venation usually not prominent, often white to yellow, and usually markedly reduced from midvein and generally discolorous and much paler, strongly glaucescent below, drying light-green to olive adaxially; reticulate venation usually inconspicuous adaxially without magnification, secondary venation usually not prominent adaxially; inflorescence to 55 cm long; fertile stems often less than 1 mm and not appearing leafy, i.e. internodes usually longer than the length of the terminal leaflet; plant often strongly twining, with stems sometimes inseparable and strongly intertwined

      8. Leaflets usually elliptic and broadest near the middle to sometimes ovate; hairs of stems dense and spreading, villous, to sometimes retrorse-spreading (to rarely retrorse-appressed strigose?); flowers 7–9 mm long; inflorescence to 15 cm long [se KS to VA, to s NY(?), e TX to GA, n FL(?)] .... ***G. regularis***

      8. Leaflets usually ovate and broadest near the base to sometimes elliptic; hairs of stems distinctly retrorse, retrorse-spreading to retrorse-appressed, hirsute to strigose; flowers 9–14 mm long; inflorescence to 55 cm long [FL to e TX, AR, and VA] .... ***G. volubilis***

    7. Mature leaflets usually with abaxial secondary venation prominent, often reddish, gradually reduced from midvein and generally concolorous and only slightly paler, only lightly glaucescent below, often drying dark brown-green to light green adaxially; reticulate venation usually conspicuous adaxially without magnification, secondary venation sometimes prominent adaxially; if venation not strongly pronounced then stems appearing leafy with short internodes subequal to the terminal leaflet length; inflorescence to 23 cm long; fertile stems ca. 1 mm wide; plant often not twining, with stems usually easily separable

      9. Most mature terminal leaflets usually > 2.5 cm long

        10. Reticulate venation strongly prominent on both surfaces, usually conspicuous on both surfaces without magnification; leaflets with pellucid, whitish microscopic dots abundant on adaxial surface; distal secondary veins mostly at near right angles or descending [pine rocklands, Miami-Dade Co., FL] .... ***G. pinetorum***

10. Reticulate venation prominent, but not strongly so, on both surfaces, usually not conspicuous abaxially without magnification and sometimes not conspicuous adaxially; leaflets with or without pellucid, whitish microscopic dots abundant on adaxial surface; distal secondary veins mostly ascending

11. Vestiture mostly villous, tomentose, to canescent [w peninsular FL to se GA, and vicinity(?)].. ***G. floridana***

11. Vestiture mostly appressed strigose [FL to NJ].............. ***G. michauxii***

9. Most mature terminal leaflets usually < 2.5 (–3.5) cm long

12. Leaflets with appressed strigose hairs adaxially; inflorescence not exserted beyond the subtending leaf; inflorescence axis 10–20 mm [w panhandle of FL, s AL, and vicinity(?)].................................. ***G. microphylla***

12. Leaflets with erect to ascending hairs adaxially; inflorescence usually exserted beyond subtending leaf, inflorescence axis (5–)20–60(–90) mm [pine rocklands, Miami-Dade Co., FL] .... ***G. smallii***

6. Stems strigose, pubescent, or hirsute; hairs appressed or oblique, not spreading; hairs often deciduous on calyx and adaxially on leaves

13. Most leaflets < 15 mm wide, < 25 mm long, leaves often overlapping with those of adjacent nodes, terminal leaflet often subequal or longer than stem internodes, leaves densely covered with pellucid, whitish microscopic dots on adaxial surface; stem vestiture antrorsely or retrorsely strigose [s MS to FL panhandle to NC]............ .... ***G. minor***

13. Most leaflets > 15 mm wide or > 25 mm long, if smaller, then leaves mostly not overlapping with those of adjacent nodes, and terminal leaflet usually shorter than the stem internodes, or if leaves smaller then pellucid, whitish microscopic dots (< 0.1 mm wide) mostly confined to veins and absent from outer leaf margin on adaxial surface; stem vestiture retrorsely hirsute or antorsely or retrorsely strigose

14. Mature leaflets with abaxial secondary venation usually not prominent, often white to yellow, and usually markedly reduced from midvein and generally discolorous and much paler, strongly glaucescent below, drying light-green to olive adaxially; reticulate venation usually inconspicuous adaxially without magnification, secondary venation usually not prominent adaxially; inflorescence to 55 cm long; fertile stems often less than 1 mm wide; plant often strongly twining, with stems sometimes inseparable and strongly intertwined

15. Leaflets consistently linear-oblong, > 4 times as long as wide (rarely with broadly elliptic leaflets), less than 7 mm wide [near pine rocklands, Miami-Dade and Monroe Cos., FL].. ***G. austrofloridensis***

15. Leaflets elliptic to ovate to narrowly ovate, some or most or all < 4 times as long as wide or more than 7 mm wide, occasionally with some leaflets > 4 times as long as wide and narrowly ovate

16. Leaflets usually elliptic and broadest near the middle to sometimes ovate; hairs of stems dense and spreading, villous, to sometimes retrorse-spreading (to rarely retrorse-appressed strigose?); flowers 7–9 mm long; inflorescence to 15 cm long [se KS to VA, to s NY(?), e TX to GA, n FL(?)] .... ***G. regularis***

16. Leaflets usually ovate and broadest near the base to sometimes elliptic; hairs of stems distinctly retrorse, retrorse-spreading to retrorse-appressed, hirsute to strigose; flowers 9–14 mm long; inflorescence to 55 cm long [FL to e TX, AR, and VA] .... ***G. volubilis***

14. Mature leaflets usually with abaxial secondary venation prominent, often reddish, gradually reduced from midvein and generally concolorous and only slightly paler, only lightly glaucescent below, often drying dark brown-green to light green adaxially; reticulate venation usually conspicuous adaxially without magnification, secondary venation sometimes prominent adaxially; inflorescence to 23 cm long; fertile stems ca. 1 mm wide; plant often not twining, with stems usually easily separable

17. Reticulate venation prominent, but not strongly so, on both surfaces, usually not conspicuous abaxially without magnification and sometimes not conspicuous adaxially; leaflets with or without pellucid, whitish microscopic dots abundant on adaxial surface; distal secondary veins usually ascending [FL to NJ] .... ***G. michauxii***

17. Reticulate venation strongly prominent on both surfaces, usually conspicuous on both surfaces without magnification; leaflets with pellucid, whitish microscopic dots abundant on adaxial surface; distal secondary veins often perpendicular, nearly so, or descending [pine rocklands, Miami-Dade Co., FL] .... ***G. pinetorum***

TAXONOMY

Galactia austrofloridensis A. R. Franck, sp. nov. Type: USA, Florida, Monroe Co., Big Pine Key, 6 Aug 1966, *Long et al. 2014* (holotype, USF). Figs 1–5.

Galactia parvifolia sensu auct., non *Galactia parvifolia* A. Rich., Hist. Phys. Cuba, Pl. Vasc. 414–415. 1845. Type of *G. parvifolia* A. Rich.: Cuba, *de la Sagra s.n.* (probable holotype, P [P00798723]).

Galactia grisebachii sensu Nesom, Phytoneuron 2015-42: 38–40. 2015, non *Galactia grisebachii* Urb., Symb. Antill. 5: 372. 1908. Lectotype of *G. grisebachii* Urb. (designated by Nesom 2015): Cuba. *Wright* "2335" (BREM; probable isolectotypes, B? [destroyed?], K, NY, US, W).

Description: Plants twining. Stems glabrate, hirsute, or strigose, hairs retrorsely oblique to appressed. Leaflets 3, linear-oblong, more than 4 times as long as wide (up to 10 times as long as wide), rarely with a few leaflets broadly elliptic and less than 4 times as long as wide, to 33 mm long and 7 mm wide, the margins usually nearly parallel for the entire length of the leaflet, rounded to emarginate at the base, rounded to emarginate to apiculate to retuse at the apex, glaucescent abaxially, adaxial reticulate venation usually inconspicuous and abaxial secondary venation usually not prominent. Inflorescence to 15 cm long or more, with a peduncle (distance to first flower node) to 4.5 cm. Flowers 8–11 mm long. Fruit to 2.5 cm long. Seeds to 3 mm long.

Galactia austrofloridensis is here established for what has long gone by the name *G. parvifolia* (Small 1933: 719; Long & Lakela 1971: 492; Isely 1998; Ward & Hall 2004) or more recently by *G. grisebachii* (Nesom 2015). The protologues and type specimens of *G. grisebachii* and *G. parvifolia* do not to apply to the plants found in Florida. In particular, the Florida plants (*G. austrofloridensis*) have long inflorescences often exserted beyond the leaves with well-spaced internodes and up to nine flowers, the rachis of which is often longer than the subtending terminal leaflet. The inflorescences of *G. grisebachii* and *G. parvifolia* are rather short and rarely exserted beyond the leaves with smaller internodes and up to five flowers, the rachis often being subequal to shorter than the subtending terminal leaflet. Narrow leaflets and short inflorescences are found on other specimens in the West Indies likely assignable to *G. grisebachii* or *G. parvifolia* e.g. from Cuba (*Britton & Gager 7683* [NY], *Britton et al. 14079* [NY], *León & Acuña 13065* [NY], *Shafer 2476* [NY]), Haiti (*Ekman H-6037* [NY]) and the Bahamas (*Correll & Correll 47675* [FTG, NY], *Correll et al. 49725* [FTG], *Hill 3360* [FTG]). Some of these specimens, like a probable isolectotype (NY) of *G. grisebachii*, have conspicuous reticulate venation, unlike *G. austrofloridensis*. The names *G. grisebachii* and *G. parvifolia* are here excluded from the Florida flora.

The protologue of *G. parvifolia* mentioned a 2–3 flowered inflorescence, pilose calyx, and villous fruit. The protologue of *G. grisebachii* (from *G. stenophylla* Urb., nom. illeg.) described a 3–5 flowered inflorescence, sparsely appressed short-pilose calyx, appressed short-pilose fruit, and noted it might be nothing but a variety of *G. parvifolia*. In the key, Urban (1900: 307–309) mentioned both had short peduncles and only distinguished *G. grisebachii* (as *G.* "stenophylla") by its equal leaflets while *G. parvifolia* had unequal leaflets that were sometimes also linear. *Galactia grisebachii* and *G. parvifolia* may be synonymous with each other as the probable isolectotype of *G. grisebachii* at NY shows variable leaflet morphology and both have short inflorescences. As noted by Nesom (2015), another collection at P (P00798722) is not *G. parvifolia* and has rather long, many-flowered inflorescences. *Dolichos filiformis* L. appears conspecific with *G. grisebachii* and/or *G. parvifolia*.

Galactia austrofloridensis is characterized by the strongly twining specimens with linear-oblong leaflets found around pine rockland habitat, mostly congruent with the distributions given by others (under the misapplied names, Long & Lakela 1971; Isely 1998; Ward & Hall 2004; Nesom 2015). *Galactia austrofloridensis* has clear affinities with *G. volubilis* (Rogers 1949: 81; Isely 1998: 569), and they both have retrorsely hirsute to strigose stem vestiture. Antrorse stem vestiture has been reported (Nesom 2015: 39), but this morphology appeared absent from the specimens seen by the present author (Appendix 1; Fig. 3). There are many specimens of *G. volubilis* in south Florida and along the coast that approach *G. austrofloridensis*, but these are usually not consistently linear-oblong and are not found near pine rocklands. Specimens of *G. volubilis* with similarly narrow leaflets usually still have predominantly ovate leaflets, narrowing towards the apex and widest below the middle. It is a rather arbitrary distinction. Since this taxon, *G. austrofloridensis*, has been recognized in the past, now at least an applicable name is available for it. Because of the obvious similarity and likely gradation between *G. austrofloridensis* and *G. volubilis*, I find it unsatisfactory to recognize *G. austrofloridensis* at the species level and am wont to use infraspecific taxonomy, or lump it into *G. volubilis* as was done by Rogers (1949). However, many other taxa of the "*G. volubilis* group" could be recognized at the infraspecific level or synonymized for the same reasons. Until relationships are better understood within the "*G. volubilis* group", *G. austrofloridensis* is reluctantly recognized.

Galactia pilosa Nutt. var. *angustifolia* Torr. & A. Gray (=*G. volubilis* var. *intermedia*, nom. illeg.) described similarly linear-oblong leaflets but no type specimen is known and no information concerning distribution was given. The varietal epithet of this name is blocked at the species level by *G. angustifolia* Kunth. As no specimens from south Florida are cited with this name (as was done with *G. spiciformis* by Torrey & Gray), it is presumed that the type specimens are not from south Florida and this name is synonymous with *G. volubilis*.

Galactia brachypoda Torr. & A. Gray, Fl. N. Amer. 1: 288. 1838. Type: USA, Florida, dry barrens, s.d., *Chapman s.n.* (holotype, NY [barcode 00008088]; probable isotype, NY ex Columbia College [barcode 00008090]). Figs. 6–7.

Galactia brachypoda has long been a perplexing name. The presumed holotype of *G. brachypoda* is a Chapman specimen at NY ([barcode 00008088]), the repository for Torrey's type specimens (Stafleu et al. 1976–1988), with the words "dry barrens" on the label, as it is congruent with the protologue phrase "dry pine barrens[.]" The probable isotype at NY came from Columbia College, a primary repository for Chapman's type specimens (Trelease 1899; Stafleu et al. 1976–1988).

The type specimens of *G. brachypoda* (Fig. 6) are similar to specimens of *G. erecta* and *G. mollis*, having corollas drying or withering to a reddish color on specimens. Of *G. brachypoda*, Rogers (1949) wrote that it "resembles *G. erecta* [...] so much that its identity is often overlooked." Isely (1986) wrote that it is "probably either a freak form of *G. erecta* or an exceptionally rare hybrid with one of the viny species." Ward & Craighead (1990) speculated it was "probably an aberrant form of the northern" *G. erecta*. Ward & Hall (2004) wrote that *G. brachypoda* is "clearly related, if not conspecific" to *G. erecta*.

On the holotype label appears to be written "*Galactia mollis*", "brevipedunculata n. sp.", and "seems to come between *G. mollis & G. sessiliflora* [*G. erecta*]". With its narrowly elliptic leaflets and petiole longer than the terminal leaflet, *G. brachypoda* appears conspecific with *G. erecta*. However, the type specimens of *G. brachypoda* also have pedunculate inflorescences with villous tips like *G. mollis*, while those of *G. erecta* are generally sessile and more strigose to glabrate. Other specimens exhibit intermediacy between typical *G. erecta* and *G. mollis*. A specimen from Baker Co., GA (*Anderson 15642*; Fig. 7) was originally identified as *G. brachypoda* and noted on the label to be erect with limited twining, sympatric with *G. erecta* and *G. mollis* (*Anderson 15645*), and possibly to be a hybrid between them. This specimen also exhibits pedunculate inflorescences. From Colquitt Co., GA, *Duncan et al. 17113* shows shortly pedunculate inflorescences and a partly twining habit. It seems likely that *G. erecta* and *G. mollis* do hybridize and apparent hybrids should be referred to as *G. brachypoda* (e.g. *Anderson 15642* and *Duncan et al. 17113*).

One other Chapman specimen at MO (acc. no. 793008) appears to be a mixed collection, with only the left specimen of the three appearing to be *G. brachypoda* (five pedunculate inflorescences, immature fruit villous, petioles seeming shorter than in *G. erecta*, stem tip curvaceous, and plant more pubescent like *G. mollis*), as annotated by Rogers. The middle and right specimen correspond with *G. erecta*, as annotated by Rogers. Though being a mixed collection, perhaps these specimens were collected at the same time and place and are indicative of *G. erecta* being involved in forming *G. brachypoda*. The label reads "*Galactia sessiliflora*" and "Wewahitchka August 1896 W. Florida" seeming to be Chapman's handwriting. On the sheet in unknown handwriting is the word "type" but if the label date is correct these cannot be type specimens. Another Chapman specimen (NY ex Sartwell Collection, Hamilton College [barcode 00008089]) was labeled *G. brachypoda* but is unlike the type specimens of *G. brachypoda* and fits well with *G. erecta* (Nesom 2015). Rogers (1949) misattributed a specimen (*Hood s.n.* [48749]) of *G. pinetorum* from Miami-Dade Co. to *G. brachypoda*, far out of the range of *G. erecta* and *G. mollis*.

It is here regarded that *G. brachypoda* Torr. & A. Gray is possibly intermediate between *G. erecta* and *G. mollis*, and that *G.* "brachypoda" sensu Nesom is misapplied. With regard to *G. brachypoda*, Isely (1986) noted "I have found no similar gatherings in any of the three major Florida herbaria (FSU, FLAS, and USF)." Similarly, I find no specimens, except the ones noted here (*Chapman s.n.*, *Anderson 15642*, and *Duncan et al. 17113*), that appear identifiable as *G. brachypoda*. Additional research is needed to determine if *G. brachypoda* is merely an occasional hybrid and/or sterile, or if it produces viable seeds and stable populations that may be rare and of conservation concern. This taxon should be searched for closely where *G. erecta* and *G. mollis* are sympatric.

Galactia erecta (Walter) Vail, Bull. Torrey Bot. Club 22: 502. 1895. *Ervum erectum* Walter, Fl. Carol. 187. 1788. Neotype (designated by Ward 2008): USA, South Carolina, Georgetown Co., 5 mi. S of Andrews, 10 Sep 1939, *Godfrey 147* (GH; isoneotypes, BH, DUKE, F, MO, NY, US). Figs. 8–9.

Glycine stricta Hook., Companion Bot. Mag. 1: 22. 1835. Type: USA, Louisiana, St. Tammany Par., Covington, *Drummond s.n.* (not located).

Galactia sessiliflora Torr. & A. Gray, Fl. N. Amer. 1: 288. 1838. Lectotype (designated by Nesom 2015): USA, Florida, *Chapman s.n.* (holotype, GH; isotypes, GH, NY).

With its erect habit and essentially sessile inflorescences, *G. erecta* is probably the most recognizable trifoliolate species of *Galactia* in the southeastern USA. Torrey & Gray (1838) suggested it may be closely related to *G. brachystachys* Benth. of Mexico.

Galactia floridana Torr. & A. Gray, Fl. N. Amer. 1: 288. 1838. Type: USA, Florida, Hillsborough Co., Tampa, "sandy places about Tampa Bay", *Dr. Burrows s.n.* (probable holotype, NY [barcode 00005288]). Figs. 10–13.

Galactia fasciculata Vail, Bull. Torrey Bot. Club 22: 505. 1895. Type: USA, Florida, Hillsborough Co., Tampa, "climbing on small shrubs", 24 Aug 1895, *Nash 2480* (holotype, NY ex Columbia College [barcode 00008083]; isotypes, AC, GH, MSC, NDG, NEB, NY, OS, P, US).

Galactia floridana Torr. & A. Gray var. *longeracemosa* Vail, Bull. Torrey Bot. Club 22: 505. 1895. Lectotype (designated by Nesom 2015): USA, Florida, 1889, *Simpson s.n.* (US; isotypes, MU, US).

Galactia volubilis var. *baltzelliana* D. B. Ward & D. W. Hall, Phytologia 86: 68. 2004. Type: USA, Florida, Lake Co., 1505 Moss Avenue, 1 mi. N of Leesburg, 25 Sep 1975, *Hall & Baltzell 413* (holotype, FLAS; isotypes, FLAS).

Galactia floridana is characterized by its densely villous-tomentose stems (Figs. 11–12) and relatively large flowers. Because of their similarities, *G. fasciculata* is here tentatively treated as a synonym of *G. floridana*. *Galactia fasciculata* was originally partly distinguished by its twining habit, compared to a non-twining habit in *G. floridana*. Curvaceous stems are common in *G. floridana* (sensu here), similar to some of the type specimens of *G. fasciculata* (e.g. NY, P). A specimen of *G. floridana* (as here identified, *Lakela 25360*) described on its label a "vine mostly prostrate under large trees," exhibiting twining similar to the US isotype of *G. fasciculata*. Three other specimens of *G. floridana* (*Lakela 25304, Lakela 25377, Schmidt 54*) described twining on their labels. Isely (1998) characterized *G. floridana* as trailing or partly twining.

The type specimen of *G. fasciculata* is evidently villous on the stem, consistent with *G. floridana*. Vail described the stems of *G. fasciculata* as "clothed with a close fine retrorse-canescent tomentum" similar to her description of *G. floridana* as often "densely and retrorsely white-tomentose". Non-twining specimens of *G. floridana* can also exhibit fasciculate inflorescences (*Franck 1218, Myers 691, Kral 7878, Thorne 48584*) and zig-zag inflorescences (*Ray 9352*), similar to the purported distinguishing characters of *G. fasciculata*. Many nodes among the type specimens of *G. fasciculata* do not have fasciculate inflorescences. The calyces of the type specimens of *G. fasciculata* appear moderately pilose to villous (described as "clothed with short, white, silky hairs" in the protologue), also found on specimens of *G. floridana*.

For *G. volubilis* var. *baltzelliana*, the type specimens (from Lake Co.) and a cited paratype (from Levy Co.) appear densely tomentose on the stem, similar to *G. floridana*. This variety was distinguished by flowers 13–21 mm long (vs. 11–14 mm in *G. floridana*), calyx 9–12 mm long (vs. 6–8 mm), and vigorously climbing or that plants "climb robustly through overlying vegetation" (vs. trailing in *G. floridana*) (Ward & Hall 2004). Other specimens of *G. floridana* have described "high twining" (*Lakela 25377*) or "twining in profusion over fallen shrub" (*Lakela 25304*) and are consistent with the morphology of *G. floridana*. It is here tentatively treated that *G. volubilis* var. *baltzelliana* is synonymous with *G. floridana*. The type specimen of *Galactia floridana* var. *longeracemosa* has dense stem vestiture and is here tentatively synonymized with *G. floridana*.

Galactia floridana probably grades into other taxa such as *G. michauxii* or *G. microphylla*. Indeed, *G. floridana* seems comparatively only more villous than *G. michauxii*, but similarly lignescent. *Galactia floridana* is very similar to *G. smallii*, a pine rockland species only marginally distinguished by its usually smaller leaflets and disjunct distribution. The leaflets of *G. floridana* seem usually to have more conspicuous reticulate venation adaxially and are usually larger than *G. microphylla* (Rogers 1949) and *G. regularis*.

Galactia floridana may be nearly endemic to Florida and southeastern Georgia. However, it is also reported from other areas but it is unclear if these specimens are possibly more related to *G. microphylla, G. minor,* or *G. regularis*. For example, the *McKenzie 264* (LSU) specimen from Louisiana seems likely to be *G. microphylla* or *G. minor*, given the rather small leaflets, short internodes, and short inflorescence (cf. Nesom 2015: 15).

Galactia michauxii A. R. Franck, sp. nov. Type: USA, Florida, Palm Beach Co., W side of US 1, Juno Beach area, 21 Apr 1962, *Lakela 24958* (holotype, USF; isotype, FSU). Figs. 14–18.

Galactia regularis sensu auct., non *G. regularis* (L.) Britton et al.

Galactia glabella sensu W. H. Duncan, Sida 8: 173–178. 1979, non *G. glabella* Michx., nom. illeg.

Galactia brachypoda sensu G. L. Nesom, Phytoneuron 2015-42: 12–15. 2015, non *G. brachypoda* Torr. & A. Gray.

Description: Plants prostrate to occasionally twining. Stems strigose, hairs retrorsely or antrorsely appressed. Leaflets 3, ovate to elliptic, less than 4 times as long as wide, to 5.5 cm long and 4.5 cm wide, the margins generally not parallel, rounded to emarginate at the base, rounded to emarginate to apiculate to retuse at the apex, only lightly glaucescent abaxially, usually with conspicuous adaxial reticulate venation and prominent abaxial secondary venation. Inflorescence to 23 cm long, with a peduncle to 7 cm long. Flowers 10–18 mm long. Fruit to 5.5 cm long. Seeds to 4 mm long.

The name *Galactia michauxii* is here established for what has been referred to as *Galactia* "regularis" (sensu auct., here regarded as misapplied), *Galactia* "glabella" (sensu Duncan, an illegitimate name), or *Galactia* "brachypoda" (sensu Nesom 2015, here regarded as misapplied), as no other specific epithet is evidently available. *Galactia michauxii* is likely equatable to *G. volubilis* sensu Ward & Hall (2004) and Wunderlin & Hansen (2008), pro parte. This species is characterized by its mostly appressed strigose stem vestiture (Figs. 16–17), leaflets with conspicuous secondary and reticulate venation (Fig. 14), inflorescence with the flowers congested near the tip, and larger flowers to 18 mm long.

As with *G. austrofloridensis*, this taxon (*G. michauxii*) had previously been recognized by improper names, and now has an available, applicable name. I had resisted giving this taxon a name, as introducing more names in *Galactia* hardly seemed like progress. I had attempted to lump it with other taxa like *G. regularis*, but that type (*Clayton 121*) with small flowers and spreading hairs does not seem applicable. The concept of *G.* "regularis" in Rogers (1949) described "prostrate or procumbent stems, occasionally twining slightly, [that are] minutely retrorse pubescent" with a mainly coastal distribution, consistent with the concept of this taxon. This taxon (*G. michauxii*) had been lumped into *G. volubilis* by others (Ward & Hall 2004; Wunderlin & Hansen 2011), but the lectotype of *G. volubilis* does not seem applicable. *Galactia floridana* could encompass this taxon, but *G. floridana* has typically been interpreted by its spreading, villous vestiture.

A proposal for conservation of *G. glabella* with perhaps its likely intended (but sterile) type specimen (P00680461) could be made. Its intended type specimen (P00680461; Fig. 15) shows conspicuous adaxial reticulate venation and prominent abaxial secondary venation, and may not be strongly twining, consistent with *G. michauxii*. The stems of P00680461 are relatively straight to curvaceous except for a leafless, strongly twining orangish stem which may not be the same taxon, possibly indicating a mixed collection or simply variability in twining. Its label has the semblance of the words "bulbos. Carolina" but has also been interpreted as "Col Co S. Carolina" to mean Colleton Co. (Duncan 1979: 175). Attempting to conserve *G. glabella* with a conserved type is problematic because of the sterile unicate type specimen (though a different type specimen could be selected, McNeill et al. 2012: Art. 14.9) and the fact that little stability would be gained for a name that has not been widely adopted or consistently applied. Thus, if this taxon (with usually prostrate stems, appressed strigose stem vestiture, and large flowers) is to have a name, it seems the best option is to make one. I here introduce the name *G. michauxii* to honor Michaux, in that his sense of *G. glabella* may have represented this taxon as interpreted by Duncan (1979). Still, *G. michauxii* is not an ideal taxon in that it seems to merge with other taxa.

Galactia floridana appears quite similar to *G. michauxii*, and seems to only differ by being villous on the stems (vs. usually appressed strigose in *G. michauxii*), while *G. pinetorum* primarily differs by its narrower leaflets and more prominent venation and *G. smallii* by its smaller leaflets and villous vestiture. The specimen *Melvin s.n.* (NCU [203568]) attributed to *G. pinetorum* (Nesom 2015) is here regarded as *G. michauxii*, which frequently has narrow leaflets but is not found in pine rocklands. Some specimens here identified as *G. michauxii* approach *G. floridana* (*Martin & Cooper 774, Woodmansee & Green 1847, Lakeal 24180, Lakela 24567*) and some are marginally separable from *G. smallii* (*Howell 1022, Lakela 24959*). Whether *G. volubilis* merges with *G. michauxii* is uncertain but probable. Duncan (1979, as *G. glabella*) and Nesom (2015, as *G. brachypoda*) both noted the peculiar antrorsely appressed forms of *G. michauxii* that were otherwise inseparable from retrorsely appressed forms. *Galactia michauxii* differs from *G. regularis* by its usually prostrate stems, appressed vestiture on the stems, and larger flowers. It differs from *G. volubilis* by its usually prostrate stems, usually elliptic leaflets with more prominent or conspicuous venation, and inflorescences with congested flowers near the apex.

Galactia microphylla (Vail) H. J. Rogers ex Isely, Brittonia 38: 354. 1986. *Galactia floridana* Vail var. *microphylla* Chapm., Fl. South. U.S. 108. 1860. Type: USA, Florida, *Chapman s.n.* (probably holotype, NY ex Columbia College [00008130]). Figs. 19–20.

Galactia microphylla has a characteristically leafy look, with rather short stem internodes similar to *G. minor* but differs by its villous stem vestiture (Fig. 20; vs. strigose in *G. minor*). Additional study is needed to determine its distribution and putative distinctions among *G. floridana*, *G. minor*, and *G. regularis*. Flowers of this species can measure to 15 mm long (e.g. *Carlton s.n.*, Appendix 1), although smaller flowers have been reported (Nesom 2015).

The authorship of this name is rather tricky. Isely (1986) credits “Rogers ex Hall & Ward” while Ward & Hall (2004) suggest the authorship should be credited to Isely, which is followed here since Isely was responsible for publishing the name. It is as if the authorship could be documented as “H.J. Rogers ex D.W. Hall & Ward ex Isely.”

Galactia minor W. H. Duncan, Phytologia 37: 59. 1977. Type: USA, Georgia, Long Co., adjacent to Altamaha River bottom SW of Ludowici, 2 Aug 1953, *Duncan et al. 16993* (holotype, GA [acc. no. 99594]; isotype, VDB). Figs. 21–23.

Similar to *G. microphylla*, *G. minor* has rather short stem internodes but differs by its strigose stem vestiture (Fig. 22). Additional study is needed to determine its relationship with *G. floridana*, *G. microphylla*, and *G. regularis*. It has been stated that *G. minor* has only antrorse stem vestiture (Duncan 1979; Nesom 2015), though a form with retrorse appressed hairs (*Demaree 35909*) is otherwise identical with *G. minor* (and here identified as *G. minor*). The notion that strigose stem vestiture can be antrorse or retrorse is also seen in *G. michauxii*.

Galactia mollis Michx., Fl. Bor.-Amer. 2: 61. 1803. Type: USA. Herb. Poiret (probable holotype, P [P00798742]). Figs. 24–25.

Eruvm volubile Walter, Fl. Carol. 187. 1788. *Galactia glabella* Michx., Fl. Bor.-Amer. 2: 62. 1803, nom. illeg. *Galactia purshii* Desv., Ann. Sci. Nat. (Paris) 9: 413. 1826, nom. illeg. Type: not designated.

Galactia pilosa Nutt., Gen. N. Amer. Pl. 2: 116. 1818. Type: USA, Georgia (holotype, PH [25556]; isotype, BM [BM001042768]).

Galactia mollis Michx. var. *nashii* Vail ex Small, Man. S.E. Fl. 720. 1933. Type: USA, Florida, Lake Co., vicinity of Eustis, Jul 1894, *Nash 880* (holotype, NY [0008093]).

The flowers that wither or dry to a reddish color (Fig. 24) and the villous immature fruits (Fig. 25) and young inflorescence tips are good characters to identify *G. mollis*. Still, many specimens of the "*G. volubilis* group" are commonly misidentified as this species. It is here regarded that the putative type specimen *Nash 880* (NY) of *Galactia mollis* var. *nashii* Vail ex Small is entirely consistent and synonymous with *G. mollis* (Small 1933: 720; Rogers 1949; cf. Nesom 2015: 12). It is also proposed that *Ervum volubile* is best regarded as a synonym of *G. mollis*.

The name *Ervum volubile* was published as "*Ervum? volubile*" for which Art. 35.2 (McNeill et al. 2012) could almost apply, "a combination is not validly published unless the author definitely associates the final epithet with the name of the genus", since Walter places a question mark next to *Ervum* suggesting an indefinite association. However, Art. 36.1 (McNeill et al. 2012) then states that a name is still validly published if accepted by the author despite the use of a question mark.

It is possible that *Ervum volubile* was meant to be a new combination from the basionym *Hedysarum volubile* L. (Nesom 2015), but this seems unlikely given that Walter did cite Linnaean basionyms in other cases where Walter placed them in a different genus than Linnaeus (e.g. *Hedera arborea* (L.) Walter, *Sophora perfoliata* (L.) Walter, *Verbesina occidentalis* (L.) Walter), in each case placing a question mark as to the genus or the Linnaean basionym. Walter may have described a new taxon, observed a twining habit, and thus proceeded to use the epithet "volubile." The lack of a known extant type specimen (see Ward 2007) and the inadequate protologue make it difficult to apply *Ervum volubile* with confidence to any taxon of *Galactia*. Though many authors have considered it a synonym of *G. regularis* or *G. volubilis*, it is conceivable that it is synonymous with *G. mollis*, for which the epithet "volubile" would also be appropriate. Walter placed only *E. volubile* and *E. erectum* (=*G. erecta*) together under his sense of *Ervum* L. and both *G. erecta* and *G. mollis* have flowers that wither or dry to a reddish color (and occur in South Carolina). The description of ovate leaflets emarginate at both ends (variable within many taxa of *Galactia*) are consistent with *G. mollis*, but the incarnate flowers seem more specific to *G. mollis* than other species in *Galactia*. Yet, even if the application of *E. volubile* were secure, the epithet is unavailable in *Galactia* since *G. volubilis* (L.) Britton is based on the same epithet. Thus, *G. mollis* Michx. still has priority within the genus.

In the protologue of *Galactia glabella* Michx., a direct quotation was made in synonymy for "*Ervum? volubile*. Walt." When published in 1803, *G. glabella*, in citing the legitimate *Ervum volubile*, must be considered illegitimate and typified by *Ervum volubile* (McNeill et al. 2012: Art. 52.1). Since the question mark was not introduced by Michaux to indicate uncertainty but was rather a quotation of the name from Walter, Art. 52.2, note 1, ex. 13 (McNeill et al. 2012) does not apply. *Galactia glabella* cannot be considered a replacement name since the epithet "volubile" was available in *Galactia* in 1803

(McNeill et al. 2012: Art. 6.4), and the epithet was only later combined into *Galactia* in 1894 based on the Linnaean basionym. *Galactia purshii* Desv., nom. illeg., also adopted the type of *E. volubile* by citing *G. glabella* (rather circuitously) (Nesom 2015).

Galactia pinetorum Small, Fl. Miami 93, 200. 1913. Type: USA, Florida, Miami-Dade Co., between Cocoanut Grove and Cutler, 9 May 1904, *Small & Wilson 1592* (holotype, NY). Figs. 26–29.

The conspicuous and strongly prominent leaflet venation (Fig. 29) are diagnostic features for *G. pinetorum*, which is confined to pine rocklands. The stems have appressed retrorse or antrorse strigose hairs (Figs. 27–28), similar to *G. michauxii*, which grades into *G. pinetorum*.

Galactia regularis (L.) Britton et al., Prelim. Cat. 14. 1888. *Dolichos regularis* L., Sp. Pl. 2: 726. 1753. Lectotype (designated by Duncan 1979): USA, "Virginia" [which included several states west and northwest of current day Virginia], *Clayton 121* (BM). Figs. 30–32.
Galactia volubilis (L) Britton var. *mississipiensis* Vail, Bull. Torrey Bot. Club 22: 508. 1895. *Galactia mississipiensis* (Vail) Rydb., Fl. Plains N. Amer. 493. 1932. Type: not designated.

Galactia regularis is slowly being more consistently applied after Duncan (1979) characterized its type specimen. The only cited element of *Dolichos regularis* (=*G. regularis*) was "Gorn. virg. 82. Habitat in Virginia." The abbreviation "Gorn." is a typographic error for Gron. or Gronovius (Nesom 2015). In Gronovius (1743: 82–83) is cited one specimen, *Clayton 121*, which is extant at BM, and Duncan (1979: 173) has been credited (Jarvis 2007: 484) with identifying it as the type specimen (lectotype). On the specimen are Latin and English descriptions and a direct citation of Gronovius (1743: 82), all evidently in the handwriting of Gronovius (Burdet s.d.).

This lectotype exhibits a twining stem and mostly elliptic leaves, broadest near the middle and rounded at both ends. Duncan (1979: 173) noted the lectotype of *G. regularis* to have "soft and spreading" hairs on the stem and its one seemingly mature flower to measure 8 mm long. Based on this Duncan realized that *G. regularis* had largely been misapplied to specimens with larger corollas and appressed stem vestiture (e.g. Rogers 1949; Isely 1998), and that the stem hairs of *G. regularis* were "uncommonly retrorse appressed." The concept of *G. mississipiensis* in Rogers (1949) seems mostly congruent with *G. regularis* in that the stem is described as having "pubescence dense, spreading or retrorse" and its distribution is mostly inland in the coastal plain.

The delimitation of *G. regularis* and *G. volubilis* is still nebulous, partly because previous interpretations of *G. volubilis* have conflicted with its lectotype. *Galactia volubilis* has been interpreted as usually having appressed stem vestiture, while its lectotype illustration is retrorsely hirsute. Additional study is needed to compare *G. regularis* and *G. volubilis* across their range, bearing in mind the necessity of matching taxonomic concepts to their type specimens.

The current interpretation of *G. regularis*, i.e. strictly similar to the lectotype (spreading hairs [Fig. 31] and flowers to 9 mm), suggests it is rare to absent in coastal areas and in peninsular Florida, which is mostly consistent with Duncan (1979) and Nesom (2015) except that both cited several specimens from Florida, Duncan mostly from north Florida and Nesom throughout the peninsula. No specimens from Florida that I have seen (Appendix 1) have the villous spreading (non-retrorse) hairs on the stem and short flowers clearly attributable to *G. regularis* s.s. Presumably, the southernmost specimens that Duncan and Nesom regarded as *G. regularis*, I am treating as *G. volubilis* (i.e. that retrorsely hirsute hairs are common in *G. volubilis*, consistent with its Dillenius lectotype). Some specimens in Florida that are retrorsely hirsute-villous with small flowers perhaps should be called *G. regularis*, e.g. *Sauleda & Ragan 5227* from Marion Co., FL. Again, the ambiguous separation between these taxa is problematic and additional observations are needed.

Forms with small flowers and elliptic leaves but retrorsely appressed hairs are here tentatively attributed to *G. regularis* and occur in north Florida (Appendix 1). In the panhandle, it may only be marginally separable from *G. microphylla* and *G. minor* which both have comparatively leafy stems. Further research is needed to determine the appropriate taxonomy for the specimens with appressed stem vestiture found in Florida that are here identified as *G. regularis* (Appendix 1). The unambiguous presence of *G. regularis* in Florida requires further study (and a veritable distinction from other taxa), especially in north Florida and the panhandle. Of the few cited specimens of *G. regularis* outside of Florida studied here (Appendix 1), most are villous with distinctly spreading hairs and do not show a retrorse pattern. However, *Hill 34955*, is villous and retrorse-spreading, with flowers ca. 9 mm long, and is here considered *G. regularis.*

Galactia smallii H. J. Rogers ex Herndon, Rhodora 83: 471. 1981. *Galactia prostrata* Small, Man. S.E. Fl. 719, 1505. 1933, nom. illeg. Lectotype (designated by Nesom 2015): USA, Florida, Miami-Dade Co., Redlands district, pinelands, 13 May 1918, *Small 8633* (NY; isolectotype, FLAS). Figs. 33–36.

Perhaps the rarest species of *Galactia* in the southeast USA is *G. smallii* (or perhaps *G. brachypoda*). *Galactia smallii* is markedly similar to *G. floridana*, both with predominantly villous stems (Fig. 34). *Galactia smallii*, a pine rockland species, is only marginally distinct by its inflorescences more pronouncedly exserted beyond the smaller leaflets, the leaflets with more conspicuous reticulate venation adaxially and abaxially, and the reticulate venation as pronounced as the secondary venation adaxially. *Galactia floridana* and *G. smallii* are separated by over 150 km. Two specimens, *Woodmansee & Hoffman 30* (FTG, USF) and *Small & Mosier s.n.* (FTG, acc. no. 93418), seem to approach *G. pinetorum* in that they are not densely villous but are somewhat antrorsely pilose.

Galactia striata (Jacq.) Urb., Symb. Antill. 2: 320. 1900. *Glycine striata* Jacq., Hort. Bot. Vindob. 1: 32. 1771. Lectotype (designated by Nesom 2015): Hort. Bot. Vindob. 1: pl. 76. 1771. Figs. 37–38.

Galactia cubensis Kunth, Nov. Gen. Sp. 6: 429. 1823. *Galactia filiformis* (Jacq.) Benth. var. *cubensis* (Kunth) M. Gómez, Anales Soc. Esp. Hist. Nat. 23: 296. 1895. *Galactia striata* (Jacq.) Urb. var. *cubensis* (Kunth) Urb., Symb. Antill. 2: 322. 1900. Type: Cuba, Havana, *Bonpland Humboldt s.n.* (holotype, P [P00660121]).

Galactia spiciformis Torr. & A. Gray, Fl. N. Amer. 1: 288. 1838. Lectotype (designated here): USA, Florida, Monroe Co., Key West, *Bennett s.n.* (NY [00008142]; isolectotype, GH [00066217]).

Galactia filiformis sensu Chapman, Fl. South. U.S. 118. 1897, non *Galactia filiformis* (Jacq.) Benth., Comm. Legum. Gen. 63. 1837 (=*Galega filiformis* Jacq., Collectanea 2: 348. 1789.) (fide Acevedo-Rodríguez & Strong 2012). Type of *Galega filiformis* at BM?

The only species currently considered here to occur in both Florida and the West Indies is *G. striata*. This species has been reported from the central-east coast of Florida (Nesom 2015), but no vouchers have been seen by the present author. Since type specimens of *G. spiciformis* exist both at NY (the presumed repository of Torrey) and GH (the presumed repository of Gray), the name is here lectotypified in accord with Rogers (1949: 106).

Galactia volubilis (L.) Britton, Mem. Torrey Bot. Club 5: 208. 1894. *Hedysarum volubile* L., Sp. Pl. 2: 750. 1753, non *Ervum volubile* Walter. Lectotype (designated by Reveal & Jarvis 2009): Dillenius, Hort. Eltham 1: pl. 143, fig. 170. Figs. 39–42.

Galactia macreei M.A. Curtis, Boston J. Nat. Hist. 1: 120. 1835. *Galactia pilosa* Nutt. var. *macreei* (M.A. Curtis) Torr. & A. Gray, Fl. N. Amer. 1: 287. 1838. Type: USA, North Carolina, *Curtis s.n.* (probable holotype, GH).

Galactia pilosa Nutt. var. *angustifolia* Torr. & A. Gray, Fl. N. Amer. 1: 287. 1838. Type: not located or designated.

Like *G. regularis*, the delimitation of *G. volubilis* is slowly becoming more consistent (Duncan 1979; Nesom 2015). There has been some discrepancy with regard to the retrorsely hirsute stem depicted on its lectotype (Duncan 1979; Nesom 2015), though it is regarded here as entirely accurate as numerous specimens of *G. volubilis* match the lectotype.

The cited elements of *Hedysarum volubile* (=*G. volubilis*) were Dillenius (1732: pl. 143, fig. 170), Linnaeus (1737: 499, no. 6), and Royen (1740: 385, no. 4). Both Linnaeus (1737: 499) and Royen (1740: 385) in turn only cited the same illustration (Dillenius 1732: pl. 143, fig. 170), which was designated the lectotype by Reveal & Jarvis (2009: 979). The application of *G. volubilis* must rely on Dillenius (1732: 173–174, pl. 143, fig. 170) and should assume an accurate description and depiction (Tjaden 1986), i.e. with a retrorsely hirsute stem, well-spaced inflorescence nodes, twining habit, and glaucescent lanceolate-ovate leaflets. There is no reason to suggest Dillenius was misrepresenting what he saw nor that retrorsely hirsute stems are atypical of *G. volubilis* (Duncan 1979; Nesom 2015).

Duncan's (1979) interpretation of *G. volubilis* relied on an uncited specimen at OXF (Nesom 2015: Fig. 5) labeled "Hedysarum trifoliatum scandens folio longiore splendente[,] H Elth 1534 1748[.]" The Latin phrase and number "1748" was probably added by Humphrey Sibthorp (1713–1797) (Druce & Vines 1897: 8) and appear consistent with his handwriting (Burdet s.d.). Sibthorp may have been responsible for the numbers in the upper right corner ("143 170 173") as another reference to Dillenius (1732). The number "173" presumably refers to the plant with the exact same Latin phrase "Hedysarum trifoliatum [...]" (Dillenius 1732: 173) with "143" and "170" identifying the associated illustration also having the exact same Latin phrase (Dillenius 1732: pl. 143, fig. 170). Stamped in the lower right corner is "Herb Sherard America" (probably added during the Druce & Vines (1897, 1907) period; Stephen Harris, pers. comm.). William Baxter (1787–1871) probably added "1534" as a sort of "Sherard Herbarium identifying number" (see Brandenburg et al. 1987; McMillan & Blackwell 2013).

There is no indication this specimen at OXF annotated by Sibthorp is a typotype, i.e. the specimen the lectotype illustration was based on. It is possible that "1748" marks the date the specimen was prepared by Sibthorp (Nesom 2015; S. Harris, pers. comm.). The year 1748 postdates Sherard's death in 1728, Dillenius (1732), and Dillenius' death in 1747. There is nothing matching the handwriting of Dillenius on the specimen (see "Linnaean Correspondence" for handwriting samples). The OXF specimen also does not bear a striking resemblance (i.e. a mirror image) in form to the illustration, as seen in other cases (see Brandenburg et al. 1987; Knapp & Jarvis 1990; Nesom 2004). As it stands, this OXF specimen cannot be used for the interpretation of the type specimen of *G. volubilis*, contrary to Duncan (1979).

Only the lectotype illustration (Dillenius 1732: pl. 143, fig. 170) and the supporting Latin descriptions (Dillenius 1732: 173–174) should be consulted for the application of *Hedysarum volubile*. Dillenius described the stem as "a sinistra dextrosum, scandentia" presumably indicating a twining habit that led to the Linnaean choice of the epithet *volubile*. The illustration exhibits lanceolate-ovate leaflets, broadest near the base, rounded at the base, and obtuse to acute at the apex. The leaflet undersides are described as "prona pallidiora and glaucescentia" (Dillenius 1732: 173). The maximum flower length is ca. 70% of the maximum leaflet width, which makes the flower seem rather small (10 mm long?) or the leaflets rather large. The inflorescence is exserted with nodes fairly well-spaced, such that the length to the second node of the inflorescence is subequal to the length from the base of the petiole to the middle of the terminal leaflet. The stem is illustrated with retrorsely hirsute hairs and is described as "tenuiter pilosa".

The majority of USF specimens cited below (Appendix 1), match perfectly well with the lectotype and its Latin descriptions, i.e. having obliquely retrorse hairs that are not strictly appressed on the stem, elongate and exserted inflorescences with well-spaced nodes, a twining habit, and glaucescent lanceolate-ovate leaflets (e.g. *Braem HI0078, Brass 20608, Caudle et al. 5292A, Caudle et al. 5292B, Caudle et al. 5744, Chicone 1086, Cole 116, Fleming 3606, Gandy DB0131, Long et al. 2328, Taylor et al. 4419, Woodbury & Roberts s.n.* [255118], *Wunderlin 9737*). Specimens with more appressed hairs on the stem but otherwise similar to the above are also frequent (e.g. *Ahles & Duke 48133, Duncan 20351, Gandy MWSR0074, Long et al. 3339*). Stem hairs of few specimens cited below are nearly all strictly appressed, and it seems common for specimens to have some hairs retrorse on the stem at an oblique angle. Many specimens cited (Appendix 1) have flowers that are subequal to the maximum leaflet width (though perhaps the largest leaflets were simply not collected), while others with larger leaflets (*Ahles & Duke 48133, Ray 11156, Ray & Lakela 11028, Shuey s.n.* [119813]) have a similar flower size to leaflet width ratio as the Dillenius lectotype.

Based on the analysis of the lectotype and the cited specimens, the concept of *G. volubilis* must allow that stems with obliquely retrorse hairs are common on specimens (Fig. 40). Contrary to the Dillenius lectotype and the above-cited specimens, others have suggested appressed hairs are common and oblique hairs are relatively rare in their delimitation of *G. volubilis* (e.g. Duncan 1979; Nesom 2015). It was also suggested that the retrorsely hirsute hairs of the Dillenius lectotype actually represented *G. regularis* (Duncan 1979; Nesom 2015) or were inaccurate exaggerations (Nesom 2015). Given that their are multiple specimens (e.g. *Braem HI0078*, etc.) that are consistent with the lectotype, the depiction of the hairs on the stem should not be interpreted as an anomaly. It is viewed here that both oblique and appressed hairs (Figs. 40–41) on the stem can be found in *G. volubilis*. In this sense, the Sibthorp OXF specimen (Nesom 2015: Fig. 5) would be compatible with *G. volubilis*. Duncan also cited two specimens that apparently exhibit retrorse-spreading hairs but still fit his sense of *G. volubilis*, *Ahles 15677* (NCU) and *Bozeman 2114* (GA).

Vail (1895: 507) observed that "This species is based on the Dillenius plate [...] and is most variable and difficult to define. The type specimen is evidently the larger leaved, long-racemed form that occurs principally from North Carolina to Florida on the coast", consistent with the distributions in Duncan (1979), Nesom (2015), and here. As noted by Nesom (2015), the distinction between the more inland *G. regularis* and the more coastal *G. volubilis* is "subtle" and "intermediates are encountered." The presumed holotype of *G. macreei* (Rogers 1949: 88, pl. 22) shows an inflorescence to ~25 cm long with well-spaced internodes, consistent with the concept of *G. volubilis.*

Some cited specimens (Appendix 1) do not seem typical of *G. volubilis*. One specimen, *Sauleda & Ragan 5227*, is retrorsely hirsute-villous, with small flowers measuring 8.2 mm long. Perhaps this specimen and other similar ones can be found in north Florida and should be called *G. regularis*. However, I hesitate to call *Sauleda & Ragan 5227 G. regularis* until additional specimens in north Florida can corroborate a morphology consistent with *G. regularis*. *Ray et al. 10809* has retrorse appressed stem vestiture with small flowers measuring 9.1 mm long. *Slaughter & Minno 12653* and *vanHoek & O'Connor CI0136* are both rather densely retrorse hirsute-villous with flowers to 11 mm. *Popenoe 1689* has conspicuous reticulate venation as if approaching *G. pinetorum*, but its leaflets are light green and strongly glaucescent like *G. volubilis*. Nesom (2015: 25) noted two specimens (*Hattaway FS0211* and *Owen FS0210*) which have rather large leaflets with conspicuous pale secondary venation abaxially and large fruits.

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Appendix 1. Specimens of trifoliolate *Galactia* examined. When no collection number is given, the barcode or accession number is provided in brackets. A question mark in brackets denotes uncertainty for the identification. All FTG and USF specimens were examined in person, while all other specimens were examined by digital image.

G. austrofloridensis: Florida: Miami-Dade Co.: *Buswell s.n.* (FTG [93423, 93424]), *Craighead s.n.* (USF [47298]), *Lakela 30212* (USF), *Reimus 99* (FTG), *Small s.n.* (FTG [93366]), *Woodbury s.n.* (FTG [93426]); Monroe Co.: *Anderson 14640* (FSU), *Gann & Bradley 498* (FTG), *Gann & Bradley 554* (FTG), *Hansen & Richardson 11448* (USF), *Karl 9* (FTG), *Koptur et al. 978, 979, 980, 981,* and *982* (FTG), *Lakela 32215* (USF), *Lakela 32215A* (USF), *Lakela & Craighead 29286* (USF), *Long & Broome 2453* (USF), *Long et al. 2014* (USF), *Poppleton & Shuey s.n.* (USF [116881]), *Robertson, Jr. s.n.* (FTG [65630, 65663]), *Sauleda & Sauleda 7039* (USF). ***G. brachypoda***: Florida: Gulf Co.: *Chapman s.n.* (MO [acc. no. 793008, mixed collection, left specimen only]). Georgia: Baker Co.: *Anderson 15642* (FSU [2 sheets], GA); Colquitt Co.: *Duncan et al. 17113* (GA). ***G. erecta***: Alabama: Mobile Co.: *Kral 39604* (JSU). Florida: *Chapman s.n.* (MO [216309]); Calhoun Co.: *Chapman s.n.* (MO [216310]); Clay Co.: *Orzell & Bridges 20102* (USF); Gulf Co.: *Chapman s.n.* (MO [acc. no. 793008, mixed collection, middle and right specimens only]); Liberty Co.: *Orzell & Bridges 19583* (FLAS, USF); Okaloosa Co.: *Carr 2014* (FLAS); Santa Rosa Co.: *Orzell & Bridges 14271* (USF). Georgia: Toombs Co.: *Duncan & Hardin 17925* (GA); Worth Co.: *Orzell & Bridges 20535* (FTG). Mississippi: George Co.: *Demaree 33419* (USF). North Carolina: Palmlico Co.: *Radford 35976* (USF). Wilmington Co.: *Williamson s.n.* (USF [93768, 93769]). ***G. floridana***: Florida: Alachua Co.: *Sauleda 5245* (USF); Charlotte Co.: *Gandy CH0007* (USF), *Wunderlin et al. 10717* (USF); Citrus Co.: *Genelle & Fleming 1535* (USF), *Hattaway FC0133* (USF), *Kral 7878* (USF), *Lakela 25166* (USF), *Lakela 25280* (USF), *Mawhinney 243* (USF), *Mawhinney 280* (USF), *Schmid A-450* (FTG, USF); DeSoto Co.: *Franck 1218* (USF); Hernando Co.: *Genelle & Fleming 927* (USF), *Lakela 24476* (USF), *Lakela 24493* (USF), *Lakela 25304* (USF), *Ray 9352* (USF), *Ray 9355* (USF), *Ray 9360* (USF), *Ray 9552* (USF); Hillsborough Co.: *Chevalier & Sreemadhavan s.n.* (USF [105237]), *Graham HR0056* (USF), *Hilsenbeck & Stenholm 17* (USF), *Lakela 25359* (FTG, USF), *Lakela 25360* (USF), *Lakela 25376* (USF), *Lakela 25377* (USF), *Lakela 30270* (USF), *Lakela 30273* (USF), *Landry & Vandaveer s.n.* (USF [222074, 223574]), *Myers 356* (USF), *Myers 691* (USF), *Ray & Lakela 10209* (USF), *Sauleda 2917* (FTG), *Schmidt 54* (FTG, USF), *vanHoek HR0639* (USF); Lake Co.: *Daubenmire & Daubenmire s.n.* (USF [179734]), *Kral 7650* (USF), *Gillis 6878* (FTG); Lee Co.: *Woodmansee & Green 1847* (FTG), *Buswell s.n.* (FTG [93140]); Levy Co.: *Orzell & Bridges 14522* (FTG); Manatee Co.: *Weber LM0040* (USF); Marion Co.: *Strong 4155* (USF); Orange Co.: *Wunderlin 5646* (USF); Pasco Co.: *Ferguson 357* (USF), *Ferguson 824* (USF), *Hood 3486* (USF), *Sauleda & Sauleda 5169* (FTG); Pinellas Co.: *Fleming 4121* (USF), *Hansen & Wunderlin 12371* (USF), *Lakela 25263* (FTG, USF), *Thorne 48584* (USF); Sumter Co.: *Strong 2093* (USF). ***G. michauxii***: Florida: Brevard Co.: *Hansen et al. 11699* (USF), *Schmalzer Aug-48* (USF), *Chicone 901* (USF), *Blissett-Clark & de Seguin des Hons s.n.* (USF [260674]), *Kennedy & Robinson 492* (USF), *MacClendon et al. 66* (USF), *MacClendon & Weichman 185* (USF); Broward Co.: *Howell 1022* (USF); Clay Co.: *Hansen & Richardson 5476* (USF), *Bridges & Orzell 23795* (USF), *Kunzer 2200* (USF); Collier Co.: *Craighead s.n.* (USF [67480]), *Lakela 28732* (USF), *Lakela 28958* (USF), *Lakela 28965* (USF), *Lakela 30825* (USF), *Lakela 30956* (FTG, USF), *Lakela 31093* (USF); Columbia Co.: *Herring & Herring 345* (USF), *Orzell & Bridges 25481* (USF); DeSoto Co.: *Shuey 2182* (USF); Glades Co.: *Franck 1478* (USF); Hendry Co.: *Sturtevant 156* (USF); Highlands Co.: *Hansen et al. 6414* (USF), *Hansen et al. 11624* (USF), *Lindsey & Upchurch 848* (USF), *Correll & Correll 52323* (FTG, USF), *Brass 33236* (USF), *Lakela 25322* (FTG, USF), *Lakela 25321A* (USF), *Hattaway et al. LJ0013* (USF), *Wunderlin & Beckner 9124* (USF), *Wunderlin & Beckner 9144* (USF), *Cole & Becker HH0062* (USF), *Christman & Simons 693* (USF); Hillsborough Co.: *Farid et al. 111* (USF), *Shuey s.n.* (USF [119854]), *Ray et al. 10135* (USF), *Myers & Myers 455* (USF), *Lakela 25894* (USF), *Lakela 29762* (USF), *Wunderlin 10688* (USF), *Landry & Vandaveer s.n.* (USF [222125]), *Ducey 126* (USF); Indian River Co.: *Bradley & Woodmansee 1108* (FTG, USF); Lake Co.: *Strong 3128* (USF), *Daubenmire & Daubenmire s.n.* (USF [203331, 239503]), *Mejeur & Walker 902* (USF); Lee Co.: *Lakela 26980* (USF), *Chicone 736* (USF), *Cole KS0025* (USF), *Woodmansee & Green 1847* (USF), *Buswell s.n.* (FTG [92935, 92936, 92939, 92940]); Levy Co.: *Skean, Jr. 843* (USF); Manatee Co.: *Becker WC0231* (USF), *Becker & Hattaway WC0311* (USF), *Dodson 8063* (USF), *Norman & Norman LM0017* (USF), *Sauleda 5037* (FTG); Marion Co.: *Martin & Cooper 477* (USF), *Martin & Cooper 774* (USF), *Long et al. 3660* (USF), *Long et al. 3661* (USF); Martin Co.: *Ray & Lakela 11087* (USF), *Popenoe & Roberts 1411* (FTG, USF), *Popenoe & Roberts 1423* (FTG), *Correll & Popenoe 48625* (FTG), *Popenoe & Popenoe 662* (FTG), *Popenoe 729* (FTG), *Popenoe et al. 1790* (FTG), *Bradley & Woodmansee 1158* (FTG), *Woodbury & Roberts s.n.* (USF [257473, 257477]); Monroe Co.: *LeDoux & Pries 450* (USF); Nassau Co.: *Longbottom 24749* (USF), *Longbottom 24751* (USF);

Okeechobee Co.: *Hansen & Robinson 8446* (USF); Orange Co.: *Popenoe 2447* (FTG, USF), *Baker s.n.* (FTG [92932]), *Buswell s.n.* (FTG [92934]), *Lakela 25988* (USF), *Wunderlin et al. 5516* (USF); Palm Beach Co.: *Lakela 24958* (USF), *Lakela 24959* (USF), *Staples III 109* (FTG); Pasco Co.: *Ferguson & Kunzer 767* (USF), *Ferguson & Kunzer 784* (USF), *Ferguson & Kunzer 854* (USF); Pinellas Co.: *Hansen et al. 12281* (USF), *Genelle & Fleming 284* (USF), *Genelle & Fleming 681* (FTG, USF), *Genelle & Fleming 2424* (USF); Polk Co.: *Hansen & Richardson 6156* (USF), *Hansen et al. 11377* (USF), *vanHoek & Wargo 915* (USF), *Lindsey & Upchurch 982* (USF), *Campbell 51* (USF), *Lakela 24180* (USF), *Lakela 24553* (USF), *Lakela 24557* (USF), *Lakela 24567* (USF), *Lakela 25149* (USF); Sarasota Co.: *Perkins s.n.* (USF [2876, 2877]), *Franck 163* (USF), *Holst et al. 5034* (USF), *Cole & Dunk OS0165* (USF); St. Johns Co.: *Slaughter 14217* (FTG); St. Lucie Co.: *Lakela 25379* (FTG, USF); Union Co.: *Williams & Williams 3821* (USF), *Sauleda 5313* (USF); Volusia Co.: *Ames 511* (FTG), *Slaughter 12417* (FTG), *Hansen & Richardson 5603* (USF), *Longbottom 12743* (USF). Georgia: Richmond Co.: *Jones 15132* (USF). North Carolina: Carteret Co.: *Grier & Czikowsky s.n.* (USF [84152]. Wayne Co.: *Duke 1027* (USF). South Carolina: Aiken Co.: *Hill & Wilson 22378* (USF); Jasper Co.: *Aulbach-Smith et al. 2682* (USF), *Daoud 49* (USF). Virginia: Nansemond Co.: *Kral 11078* (USF); Sussex Co.: *Seymour 91 7 20* (USF). ***G. microphylla***: Florida: Escambia Co.: *Carlton s.n.* (USF [162778]). Gulf Co.: *Orzell & Bridges 15340* (FTG); Okaloosa Co.: *Godfrey 68914* (FSU); Santa Rosa Co.: *Crewz 1136* (USF). ***G. minor***: Alabama: Baldwin Co.: *Kral 35773* (USF); Florida: Bay Co.: *Grey s.n.* (USF [233066]); Escambia Co.: *Kral & Godfrey 6064* (USF); Santa Rosa Co.: *Barghoorn 29* (USF); Washington Co.: *Keppner s.n.* (FSU [206328]). Georgia: McIntosh Co.: *Bozeman 1064* (USF); Randolph Co.: *Orzell & Bridges 18043* (FTG). Louisiana: Cameron Par.: *McKenzie 264* (LSU) [?]. Mississippi: George Co.: *Demaree 33492* (USF); Harrison Co.: *Demaree 32398* (USF), *Demaree 32436A* (USF), *Ray 2932* (USF); Jackson Co.: *Demaree 33933* (USF). ***G. mollis***: Alabama: Bullock Co.: *Dykes 1631* (TROY, UWAL), *Diamond 19425* (TROY). Florida: Alachua Co.: *Holland & Mears s.n.* (USF [204224]), *Zomlefer 629* (FTG); Clay Co.: *Orzell & Bridges 20107* (USF), *Sauleda & Ragan 5606* (FTG, USF); Flagler Co.: *Popenoe et al. 1729* (FTG); Hillsborough Co.: *Lakela 25133* (USF), *Lakela 25144* (USF), *Lakela 25193* (USF); Lake Co.: *Daubenmire & Daubenmire s.n.* (USF [179710]), *Mejeur & Walker 901* (USF), *Nash 880* (NY), *Taylor s.n.* (USF [208399]), *Baker s.n.* (FTG [93395]); Marion Co.: *Hubbard 570* (USF), *Long et al. 3663* (USF); Orange Co.: *Buswell s.n.* (FTG [93399]); Polk Co.: *Buswell s.n.* (FTG [93398]); Sumter Co.: *Wunderlin et al. 9783*; Suwannee Co.: *Herring & Herring 862* (USF); Volusia Co.: *Ames 509* (FTG), *Ames 515* (FTG); Wakulla Co.: *Anderson 23888* (FSU). Georgia: Baker Co.: *Anderson 15645* (FSU). North Carolina: Cumberland Co.: *Ahles & Haesloop 29747* (FSU, USF). South Carolina: Williamsburg Co.: *Orzell & Bridges 24965* (USF). ***G. pinetorum***: Florida: Miami-Dade Co.: *Austin & Nauman 6935* (FTG), *Austin & Nauman 6939* (FTG), *Avery 1187* (FTG), *Bradley 713* (FTG), *Bradley 1653* (FTG), *Bradley 1670* (FTG, USF), *Britton s.n.* (USF[192046]), *Broome s.n.* (USF [75281, 75282, 76482]), *Buswell s.n.* (FTG [93400, 93401, 93402, 93404, 93406, 93411, 93416]), *Correll 49925* (FTG), *Craighead s.n.* (USF [47273]), *Craighead 719* (FTG), *Eaton 987* (USF), *Fawcett s.n.* (FTG [23455]), *Hill 2979* (FTG), *Hood s.n.* (FLAS [48749]), *Lakela 27269* (USF), *Lakela 28773* (USF), *Lakela 28438* (USF), *Lakela & Craighead 25734* (USF), *Lakela & Long 29704* (USF), *Moldenke s.n.* (FTG [92938]), *Nauman & Austin 770* (FTG), *Nauman & Austin 774* (FTG), *Nauman & Austin 777* (FTG), *Possley & Fellos 15* (FTG), *Skinner s.n.* (FTG [161913]), *Small s.n.* (USF [17695]), *Small s.n.* (FTG [93405]), *Small & Mosier s.n.* (FTG [93403]), *Small & Mosier s.n.* (FTG [93149]), *Woessner 175* (FTG), *Woessner s.n.* (FTG [93407]), *Woodbury s.n.* (FTG [93411]). ***G. regularis***: Florida: Calhoun Co.: *MacClendon et al. 1304* (USF) [?]; Gadsden Co.: *Anderson 26557* (FSU) [?]; Jackson Co.: *Anglin s.n.* (USF [255832]) [?];

Jefferson Co.: *Godfrey 67374* (FSU) [?]. Georgia: Floyd Co.: *Duncan 17183* (USF). Illinois: Union Co.: *Hill 34955* (USF). Kentucky: Powell Co.: *Wharton 5705* (USF). Louisiana: Catahoula Par.: *Thomas et al. 10854* (USF); Union Par.: *Taylor et al. 4602* (USF). Mississippi: Jackson Co.: *Seymour 49* (USF); Lowndes Co.: *Ray 7324* (USF); Pike Co.: *Ray 5675* (USF); Wilkinson Co.: *Ray 5498* (USF). Missouri: Scott Co.: *Yatskievych et al. 15-124* (MO); Stoddard Co.: *Davidse 42569* (MO). New Jersey: Cape May Co.: *Brown s.n.* (USF [288430]). North Carolina: Durham Co.: *Biersacki s.n.* (FTG [35750]); Washington Co.: *Radford 38747* (USF). South Carolina: Union Co.: *Hill 25889* (USF). Tennessee: Rutherford Co.: *Hill 30684* (USF). ***G. smallii***: Florida: Miami-Dade Co.: *Avery 2164* (FTG, USF), *Avery 2229* (FTG, USF), *Franck 3923* (USF), *Lakela 28766* (USF), *Woodmansee & Hoffman 30* (FTG, USF), *Austin & Nauman 6928* (FTG), *Woodbury & Buswell s.n.* (FTG [03438]), *Woodbury s.n.* (FTG [93414]), *Fanning & McMahon 422* (FTG), *Avery 2096* (FTG), *Woodmansee 603* (FTG), *Small & Mosier s.n.* (FTG [93418]). ***G. striata***: Florida: Charlotte Co.: *Gandy CH0053* (USF); Collier Co.: *Correll & Popenoe 53229* (USF), *Lakela 29444* (USF), *Lakela 31240* (USF), *Lakela & Almeda 30094A* (USF), *Lakela & Laker 29095* (USF), *Lakela et al. 31404* (USF), *Long 1477* (USF); *Tuthill s.n.* (FTG [92943]) Lee Co.: *Brumbach 6594* (USF), *Brumbach 7724* (FTG, USF), *Hansen et al. 4997* (USF), *Todd 91* (USF), *Wunderlin et al. 6109* (USF), *Wunderlin et al. 6249* (USF); Miami-Dade Co.: *Long et al. 1918* (USF), *Buswell s.n.* (FTG [03439]), *Bradley 1347* (FTG); Monroe Co.: *Aregood 115* (USF), *Byrd s.n.* (USF [286016]), *Carlton s.n.* (USF [162541]), *Craighead s.n.* (USF [64181]), *Cooley et al. 6221* (USF), *Cooley et al. 9250* (USF), *Correll & Long 40967A* (FTG), *Dawes & Croley s.n.* (USF [79386]), *Hansen & Richardson 11443* (USF), *Hansen et al. 10670* (USF), *Hetzell 41* (USF), *Lakela 27847* (USF), *Lakela et al. 28623* (USF), *Lakela et al. 31780* (USF), *LeDoux & Pries 485* (USF), *Long 2010* (USF), *Long 3012* (USF), *Long & Broome 2479* (USF), *Long & Wunderlin 4086* (USF), *Long et al. 1819* (USF), *Long et al. 2805* (USF), *Long et al. 2686* (USF), *Longbottom & Williams 5465* (USF), *Poppleton 790* (USF), *Poppleton & Shuey s.n.* (USF [116316]), *Stalter 82* (USF); Sarasota Co.: *Lakela & Long 27559* (USF). ***G. volubilis***: Florida: Brevard Co.: *Shuey M0168* (USF), *Shuey & Poppleton s.n.* (USF [125434]), *Hansen 11895* (USF), *Poppleton M1468* (USF), *Lakela 27650* (USF), *Long et al. 2345* (USF), *Slaughter & Minno 12653* (FTG); Broward Co.: *Howell 946* (USF), *Howell 1302* (USF), *Tabb s.n.* (FTG [122181]); Charlotte Co.: *Franck 2823* (USF); Citrus Co.: *Williams & Longbottom 3116* (USF), *Ray & Lakela 11028* (USF), *Schmid A449* (USF), *Schmid A-62* (USF), *Lakela et al. 26036* (USF), *Lakela et al. 30189* (USF); Collier Co.: *Hetzell 23* (USF), *Correll et al. 51775* (USF), *Owen FS0210* (USF), *Lakela & Laker 29135* (USF), *Hattaway FS0211* (USF), *Sauleda & Sauleda 8763* (USF), *Popenoe 1326* (FTG); Columbia Co.: *Amoroso & Tan 44* (USF), *Tan 22* (FTG); DeSoto Co.: *Fulton 32* (USF), *Fulton 172* (USF), *Fulton 327* (USF), *Franck 868* (USF); Gilchrist Co.: *Hansen et al. 10840* (USF); Hardee Co.: *Farid & O'Donovan 8* (USF), *Brass 20608* (USF), *Cole PC0035* (USF); Hernando Co.: *Hansen & Richardson 6220* (USF), *vanHoek 31* (USF), *Lakela 24437* (USF), *Lakela 24480* (FTG, USF), *Lakela 25302* (USF), *Genelle & Fleming 998* (USF); Hillsborough Co.: *Arcuri 252* (USF), *Arcuri 450* (USF), *Shuey s.n.* (USF [119813]), *Crutcher 3* (USF), *Caudle et al. 2413* (USF), *vanHoek & Parsons HR0587* (USF), *Crewz & Kutash 1469* (USF), *Lakela 26254* (USF), *Lakela 30130* (USF), *Chicone 1086* (USF), *Ducey 127* (USF); Indian River Co.: *Wunderlin & Beckner 6472* (USF), *Long et al. 3569* (USF), *Long et al. 3571* (USF), *Meagher 1458* (FTG); Jackson Co.: *Hansen & Essig 11460* (USF), *Godfrey & Gholson 81551* (FTG); Lafayette Co.: *Caudle et al. 5744* (USF), *Caudle et al. 5292A* (USF), *Caudle et al. 5292B* (USF); Lake Co.: *Hansen et al. 11912* (USF), *Daubenmire & Daubenmire s.n.* (USF [178025, 211485]), *Rochow s.n.* (USF [150710]); Lee Co.: *Radford & Leonard 45549* (NCU), *Hansen & Hansen 5676* (USF), *Brown s.n.* (USF [177018, 188017]), *Phillips et al. 200* (USF), *Anderson & Jamison LK0081* (USF), *Todd 45* (USF), *Braem GI0169*

(USF), *Webb et al. 2* (USF), *Avery 1948* (FTG); Leon Co.: *Godfrey 72826* (TTRS); Levy Co.: *Hansen & Richardson 5972* (USF), *Crewz & Wain 1634* (USF), *Gulledge 372* (USF), *Long et al. 3339* (USF); Madison Co.: *Hansen & Essig 11579* (USF); Manatee Co.: *Hansen & Hansen 5803* (USF), *Becker WC0548* (USF), *Cole 116* (USF); Marion Co.: *Sauleda & Ragan 5227* (USF), *Wunderlin et al. 9905* (USF); Martin Co.: *Woodbury & Roberts s.n.* (USF [255118]), *Woodmansee 763* (FTG, USF); Miami-Dade Co.: *Lakela & Almeda 31856* (USF), *Correll et al. 50524* (FTG), *Popenoe 1689* (FTG); Monroe Co.: *Byrd s.n.* (USF [286015]), *Wiggins 20079* (USF), *Lakela & Long 28581* (USF), *Lakela & Long 28581* (USF), *Longbottom & Williams 5448* (USF), *Correll & Correll 50358* (FTG); Nassau Co.: *Popenoe 2080* (FTG, USF); Orange Co.: *Cheak 74* (USF); Palm Beach Co.: *Hansen et al. 7119* (USF); Pasco Co.: *Hansen et al. 9896* (USF); Pinellas Co.: *Hansen et al. 12807* (USF), *vanHoek & O'Connor CI0136* (USF), *Hilbert 136* (USF), *Fleming 3281* (USF), *Fleming 3606* (USF), *Fowler 57* (USF), *Lakela et al. 26315* (USF), *Lakela 26707* (USF), *Lakela 27363* (USF), *Genelle & Fleming 3212* (USF), *Braem HI0078* (USF), *Perkins et al. 56* (USF), *Woodbury s.n.* (FTG [92927]); Polk Co.: *Conard s.n.* (USF [66368, 76515]), *Gilbert s.n* (USF [288224])., *Jennings & Jennings s.n.* (USF [55696]), *Rochow s.n.* (USF); Sarasota Co: *Dodson 4627* (USF), *Gandy MWSR0074* (USF); Seminole Co.: *Williams 3301* (USF), *Williams 3304* (USF); St. Lucie Co.: *Hansen et al. 7131* (FTG, USF), *Lakela 25233* (USF), *Wunderlin et al. 10157* (USF); Sumter Co.: *Hansen & Robinson 9612* (FTG, USF), *Gandy DB0131* (USF), *Wunderlin et al. 9737* (USF), *Rochow s.n.* (USF [150713, 153773]); Volusia Co.: *Hansen & Robinson 8264* (USF), *Kunzer 1921* (USF), *Correll & Correll 52748* (FTG, USF), *Ray et al. 10809* (USF), *Ray 11156* (USF), *Long et al. 2322* (USF), *Long et al. 2328* (USF), *Longbottom 16316* (NY, USF). Louisiana: Caldwell Par.: *Taylor et al. 4419* (USF); Union Par.: *Taylor et al. 4592a* (USF). Georgia: Long Co.: *Bozeman 2114* (GA); McIntosh Co.: *Duncan 20351* (USF). Mississippi: Hancock Co.: *Hermann 398* (USF); Jackson Co.: *Demaree 36052* (USF). North Carolina: Pasquotank Co.: *Ahles & Duke 48133* (USF).

Appendix 2. Figures 1–42. The blue ruler in the photos is in millimeter increments.

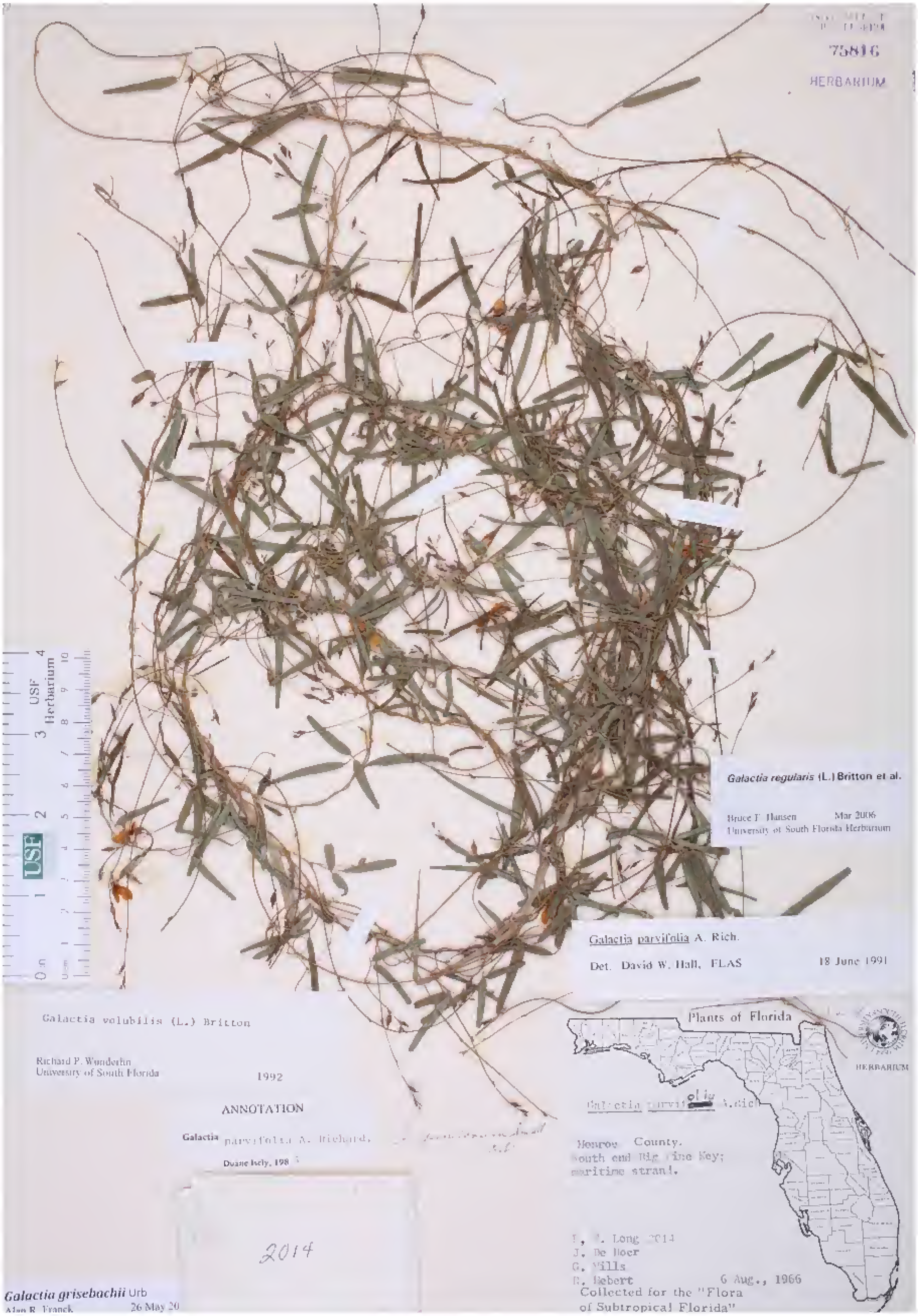


Figure 1. Holotype of *Galactia austrofloridensis* (*Long et al. 2014*).

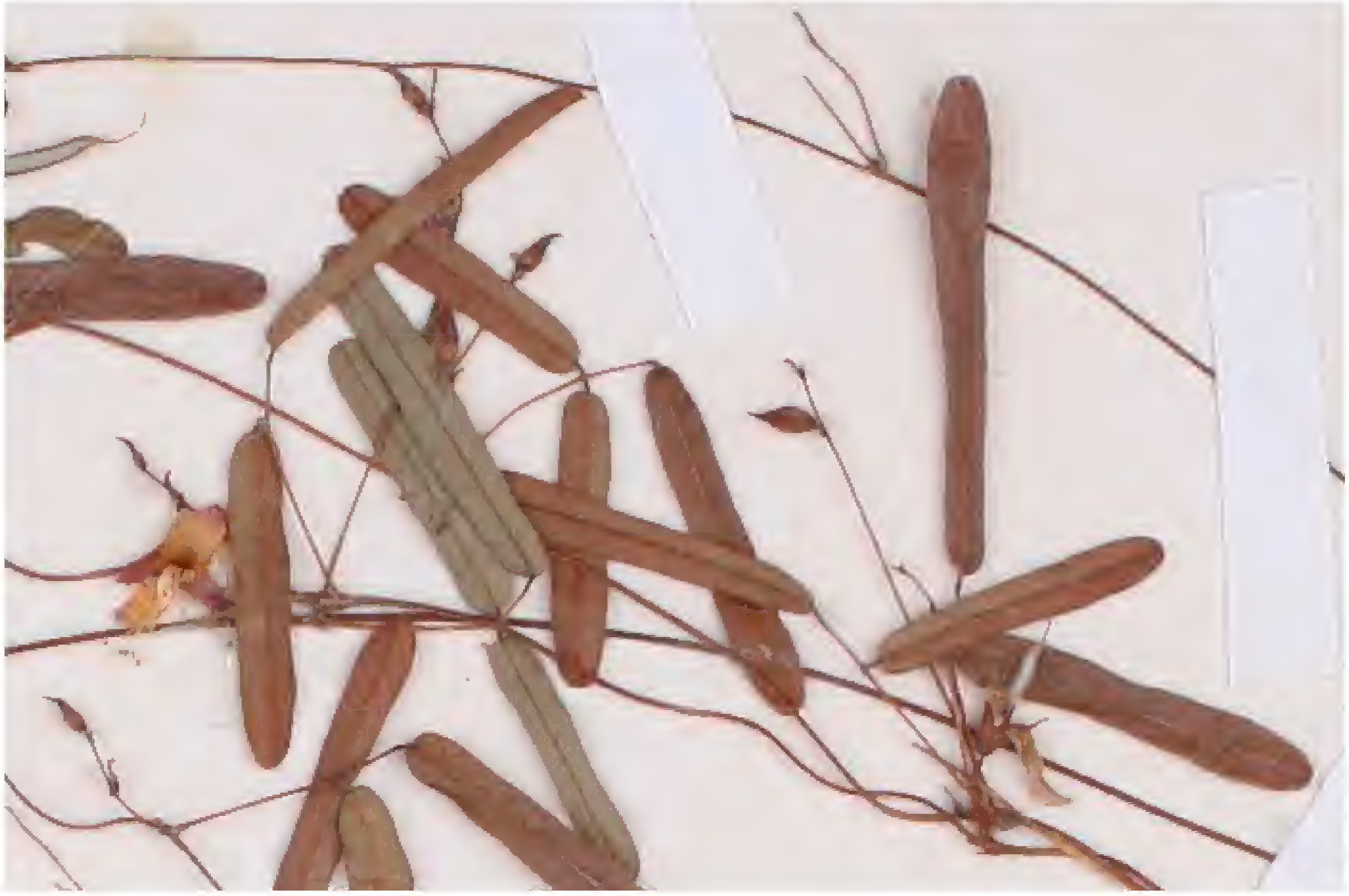


Figure 2. *Galactia austrofloridensis* (*Lakela 30212*).

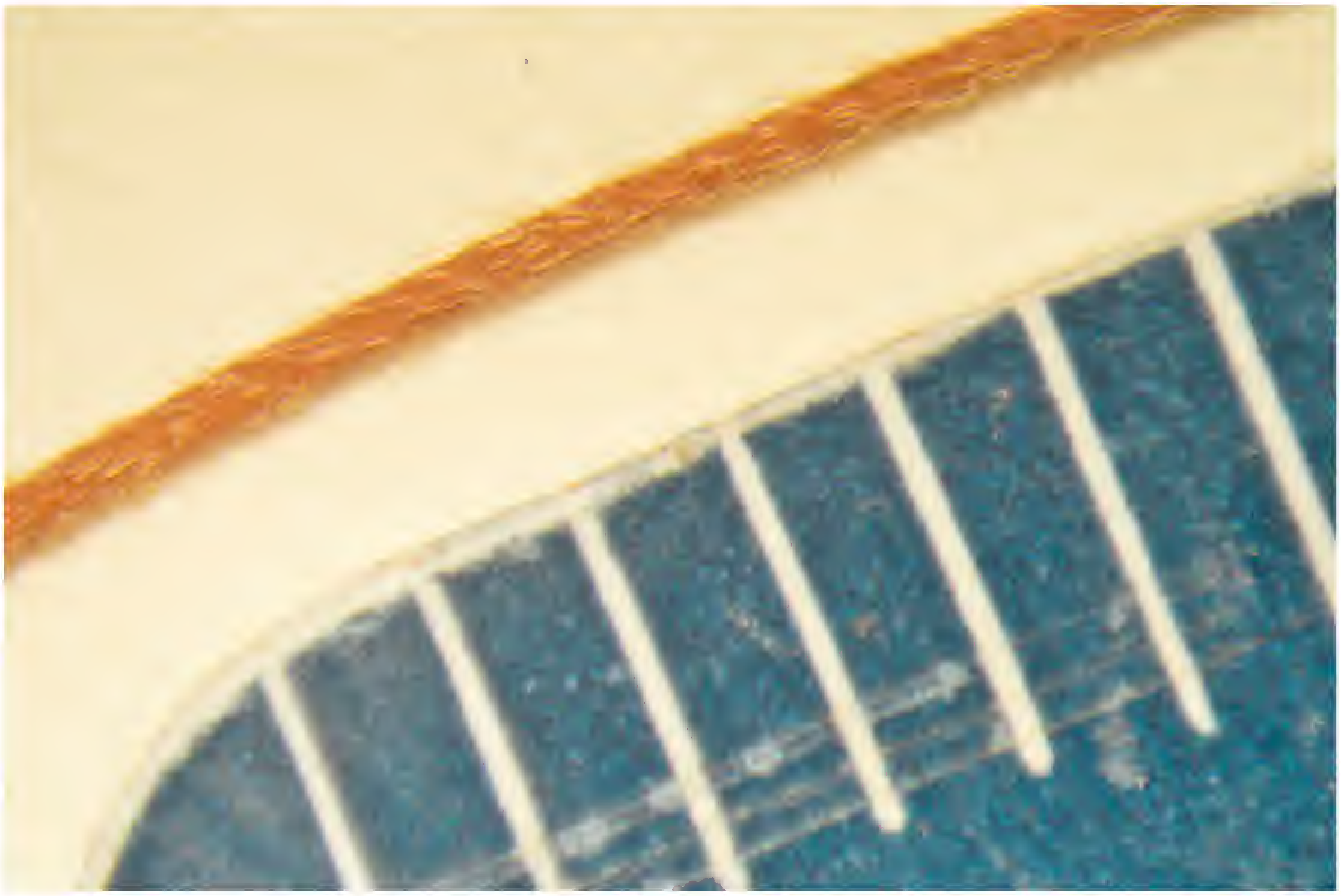


Figure 3. *Galactia austrofloridensis*, with a retrorsely strigose stem (*Sauleda & Sauleda 7039*). The distal portion of the stem is towards the upper right.

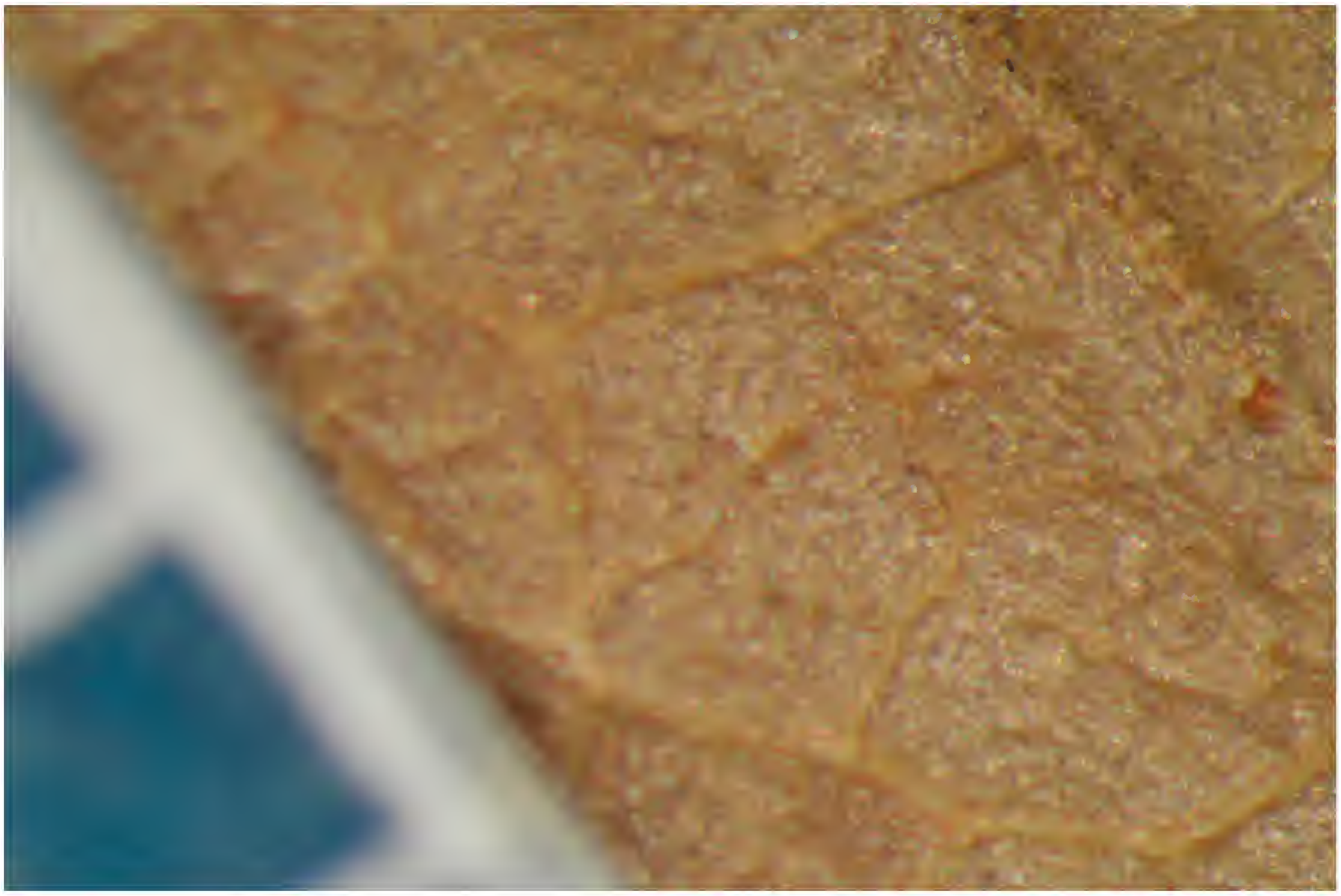


Figure 4. *Galactia austrofloridensis*, with a few pellucid dots confined to the midrib of the leaflet (*Craighead s.n.* [47298]).

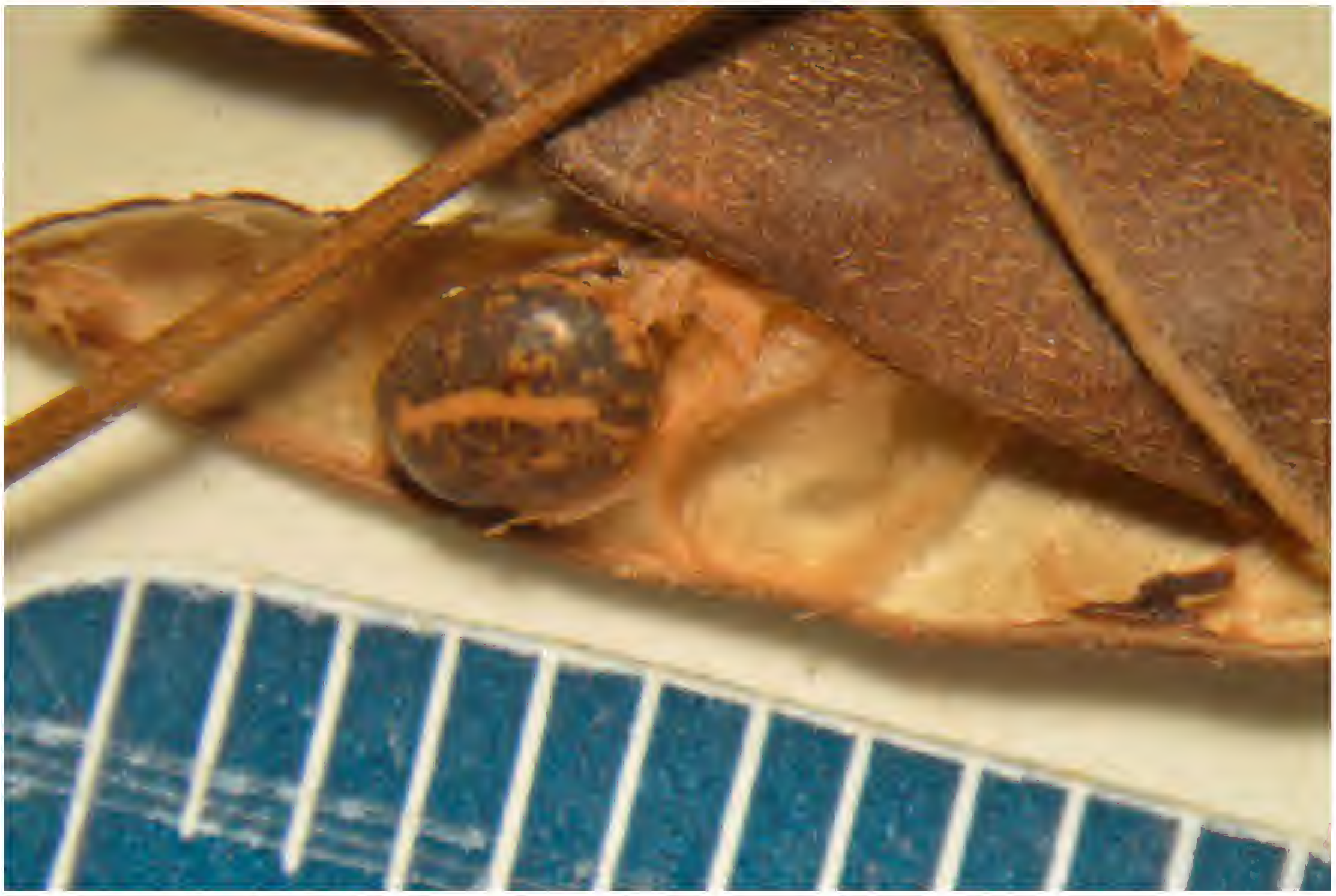


Figure 5. *Galactia austrofloridensis*, seed attached to the fruit (*Lakela 32215A*).

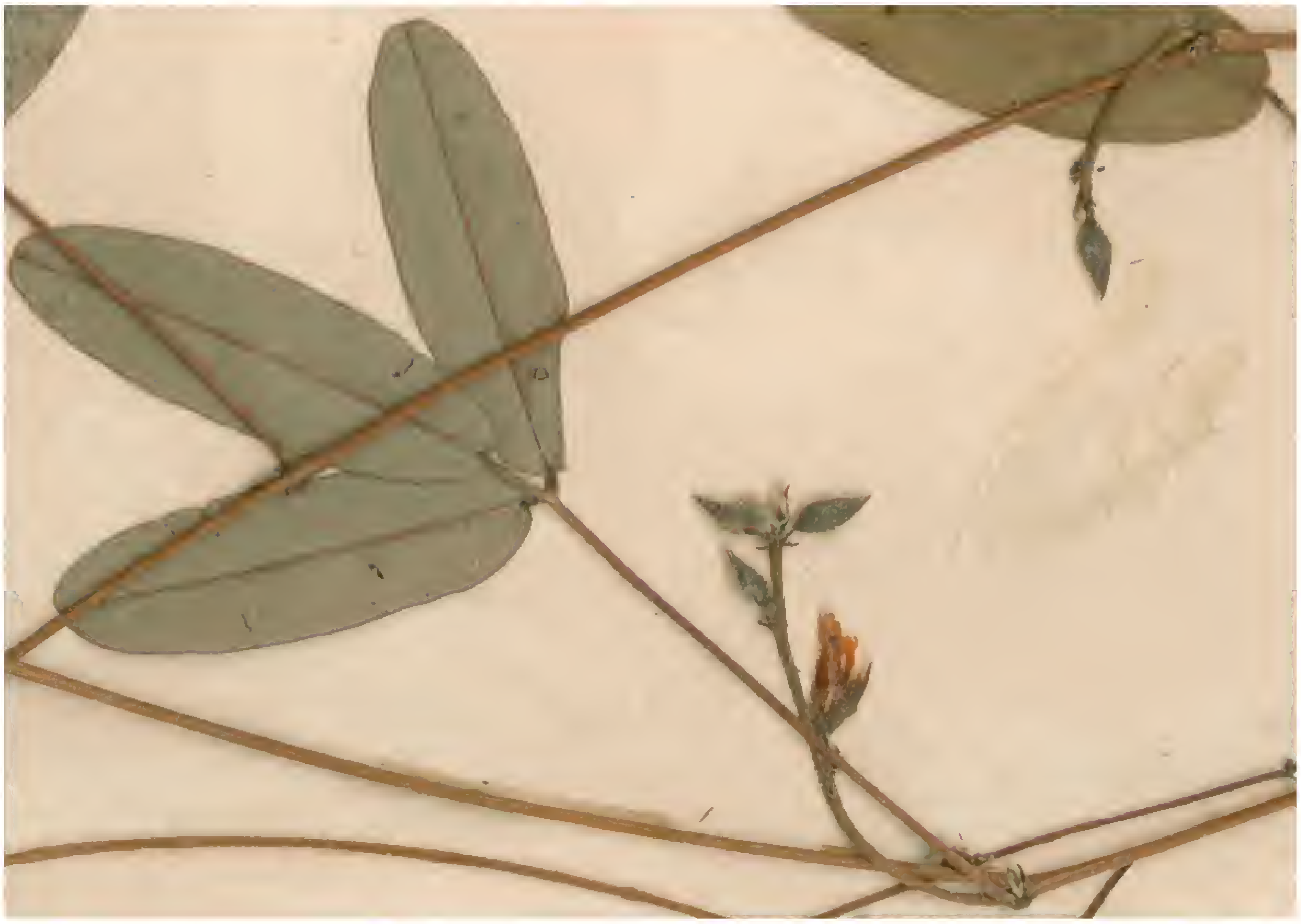


Figure 6. Probable holotype of *Galactia brachypoda* (NY, 00008088). This image belongs to The C. V. Starr Virtual Herbarium (http://sweetgum.nybg.org/science/vh/); used with permission.

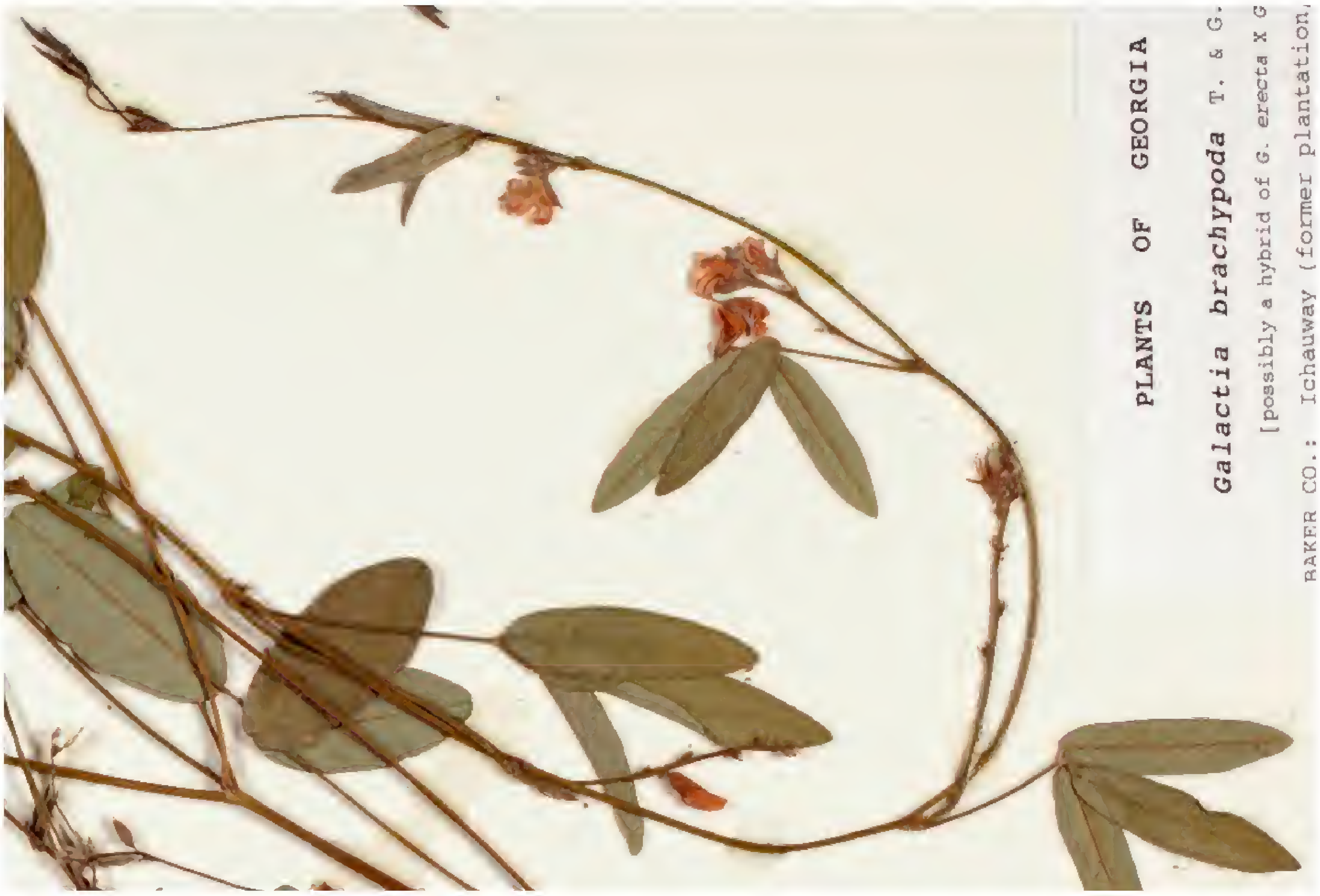

PLANTS OF GEORGIA
Galactia brachypoda T. & G.
[possibly a hybrid of G. erecta X G
BAKER CO.: Ichauway (former plantation,

Figure 7. *Galactia brachypoda* (Anderson 15642, FSU). Image courtesy of the Florida State University's Robert K. Godfrey Herbarium.

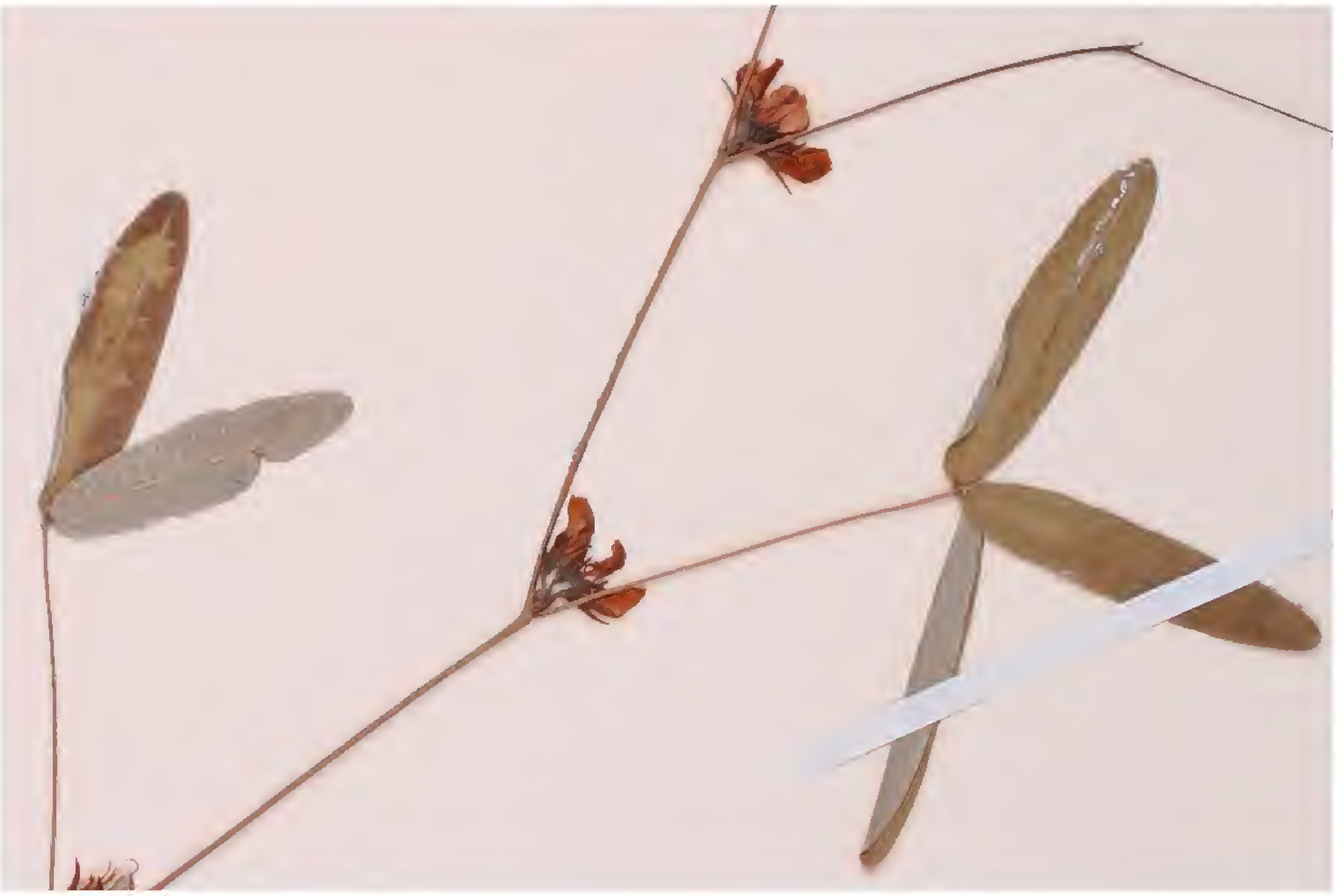


Figure 8. *Galactia erecta* (*Williamson s.n.* [93768]).

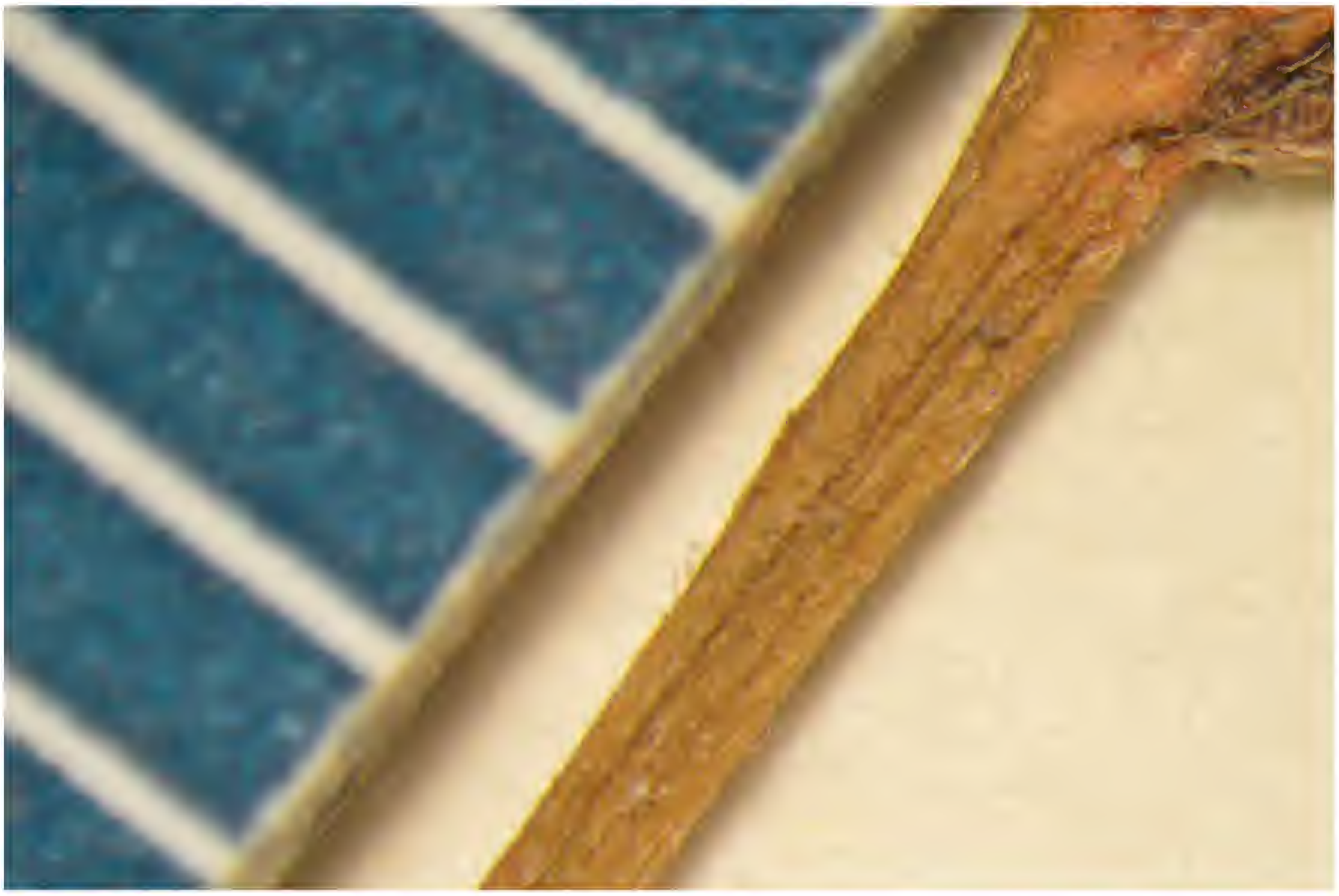


Figure 9. *Galactia erecta*, with an antrorsely sparsely strigose stem (*Orzell & Bridges 20102*). The distal portion of the stem is towards the upper right.

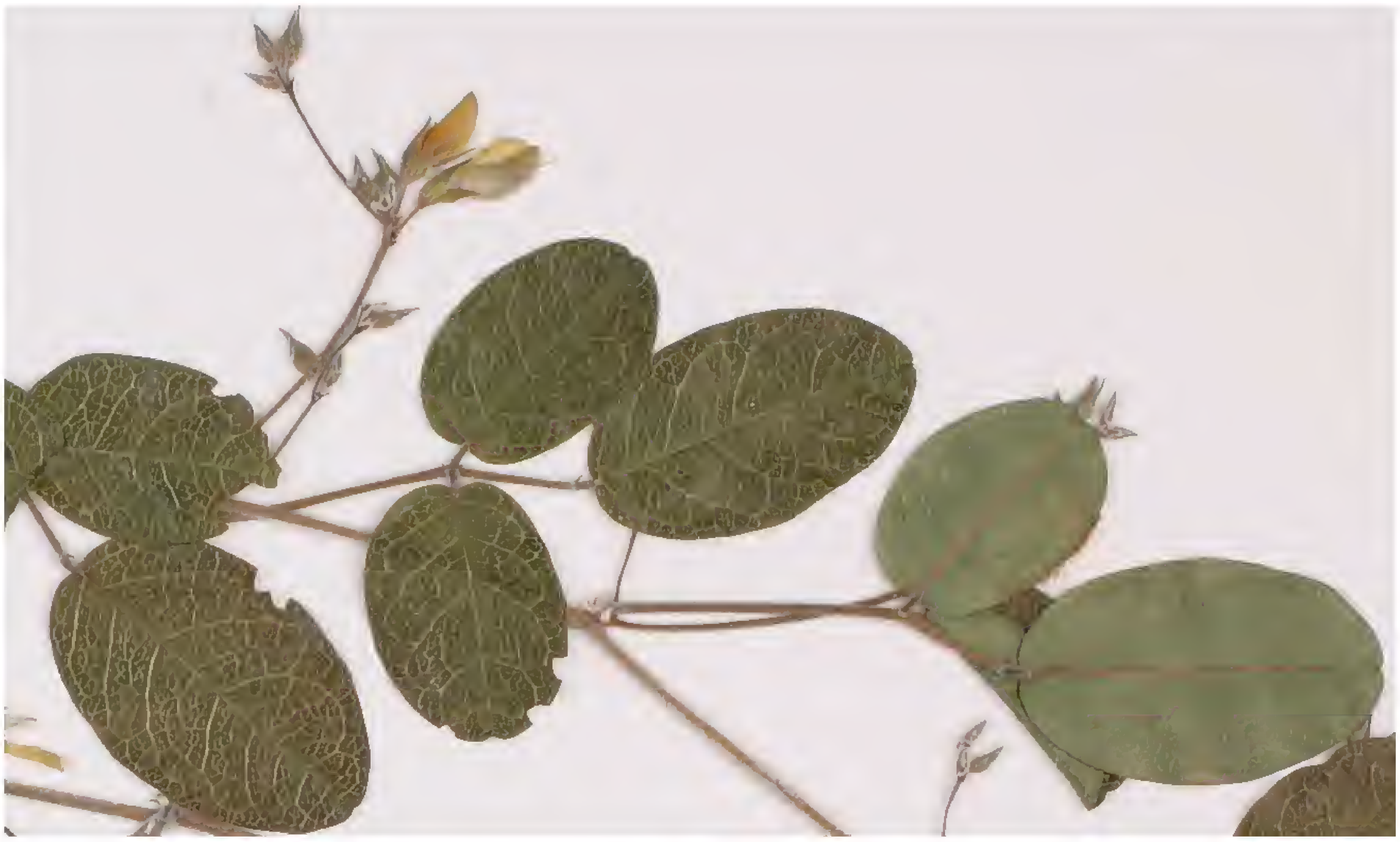


Figure 10. *Galactia floridana* (*Franck 1218*).

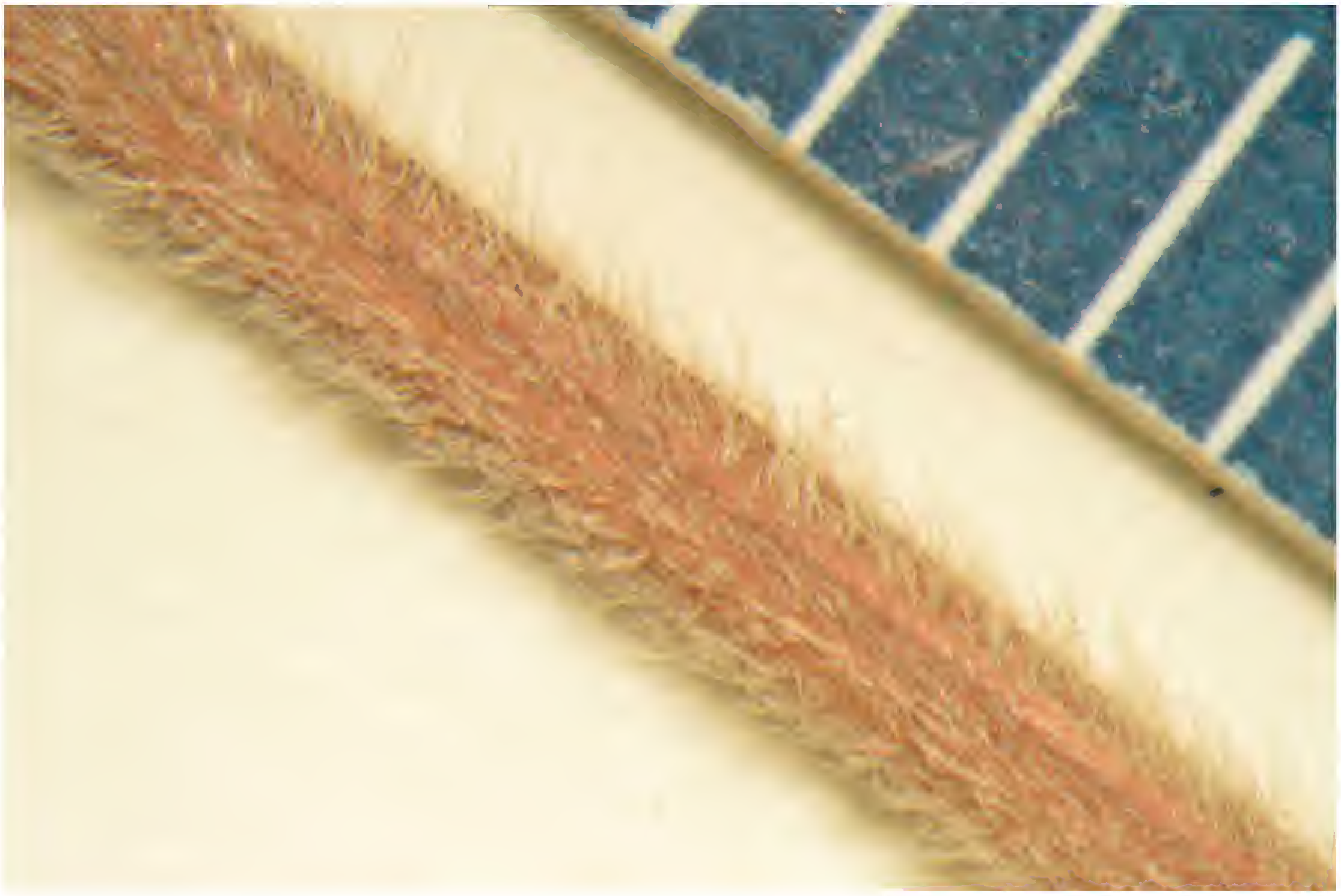


Figure 11. *Galactia floridana*, with an antrorsely villous stem (*Myers 691*). The distal portion of the stem is towards the upper left.

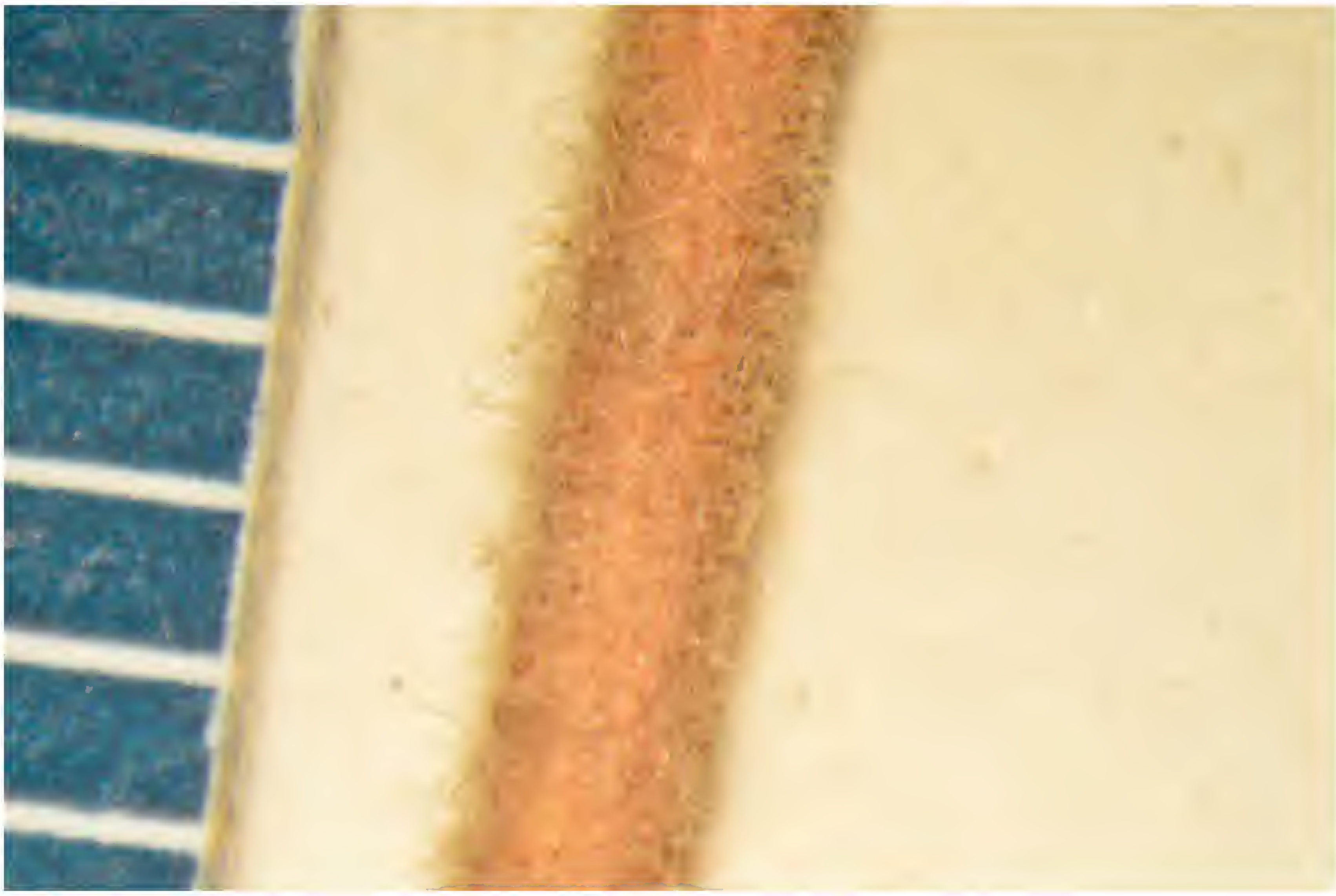


Figure 12. *Galactia floridana*, with a villous stem (*Lakela 25359*). The distal portion of the stem is towards the top.

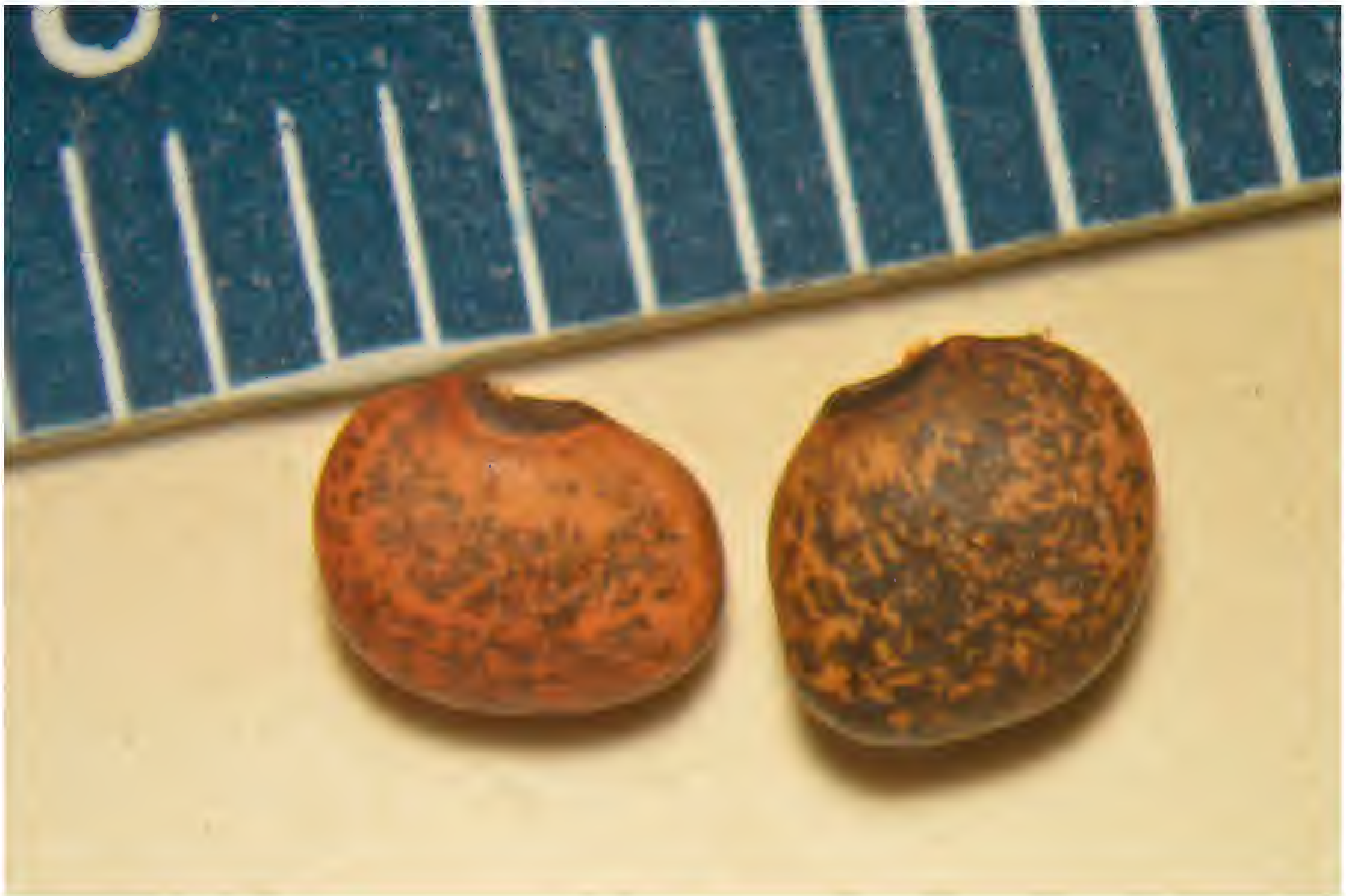
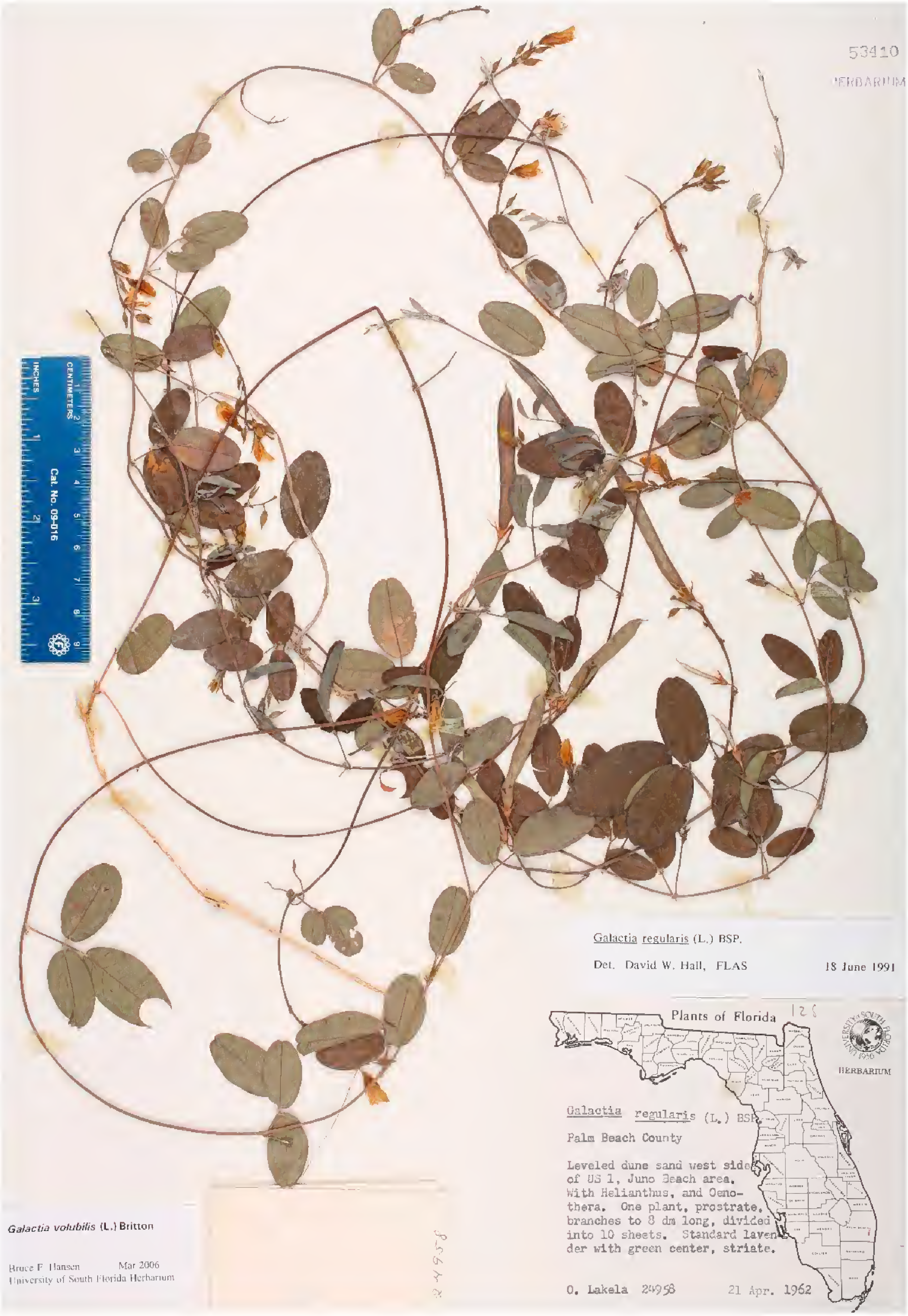


Figure 13. *Galactia floridana*, seeds (*Ray 9552*).



Galactia regularis (L.) BSP.
Det. David W. Hall, FLAS 18 June 1991

Plants of Florida

Galactia regularis (L.) BSP.
Palm Beach County

Leveled dune sand west side of US 1, Juno Beach area. With Helianthus, and Oenothera. One plant, prostrate, branches to 8 dm long, divided into 10 sheets. Standard lavender with green center, striate.

O. Lakela 24958 21 Apr. 1962

Galactia volubilis (L.) Britton

Bruce F. Hansen Mar 2006
University of South Florida Herbarium

Figure 14. Holotype of *Galactia michauxii*, *Lakela 24958* (USF).

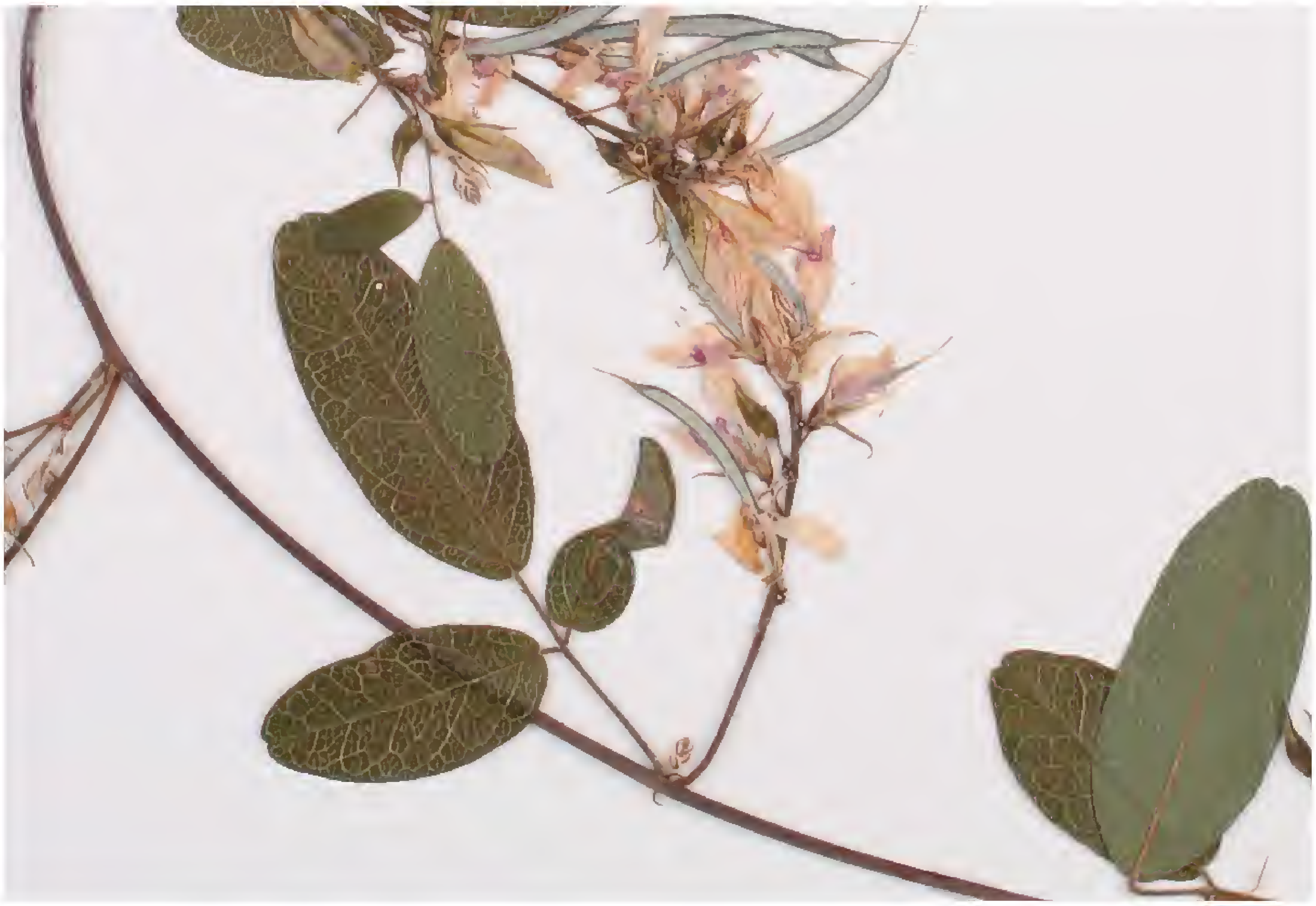


Figure 14. *Galactia michauxii* (*Longbottom 12743*).

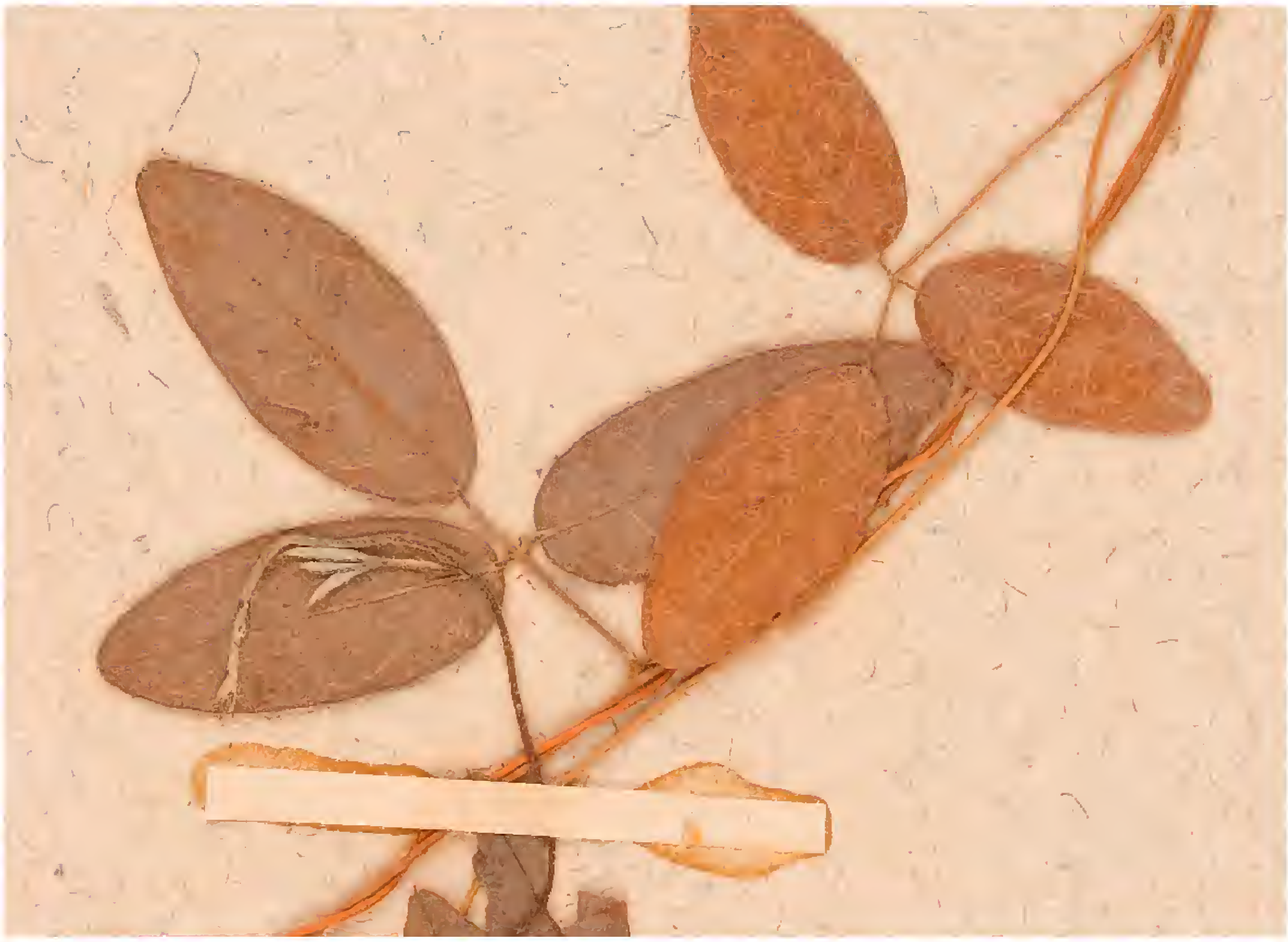


Figure 15. Possibly *Galactia michauxii*, and the likely intended type specimen of *G. glabella*, nom. illeg, at P, copyright MNHN - Herbier National.

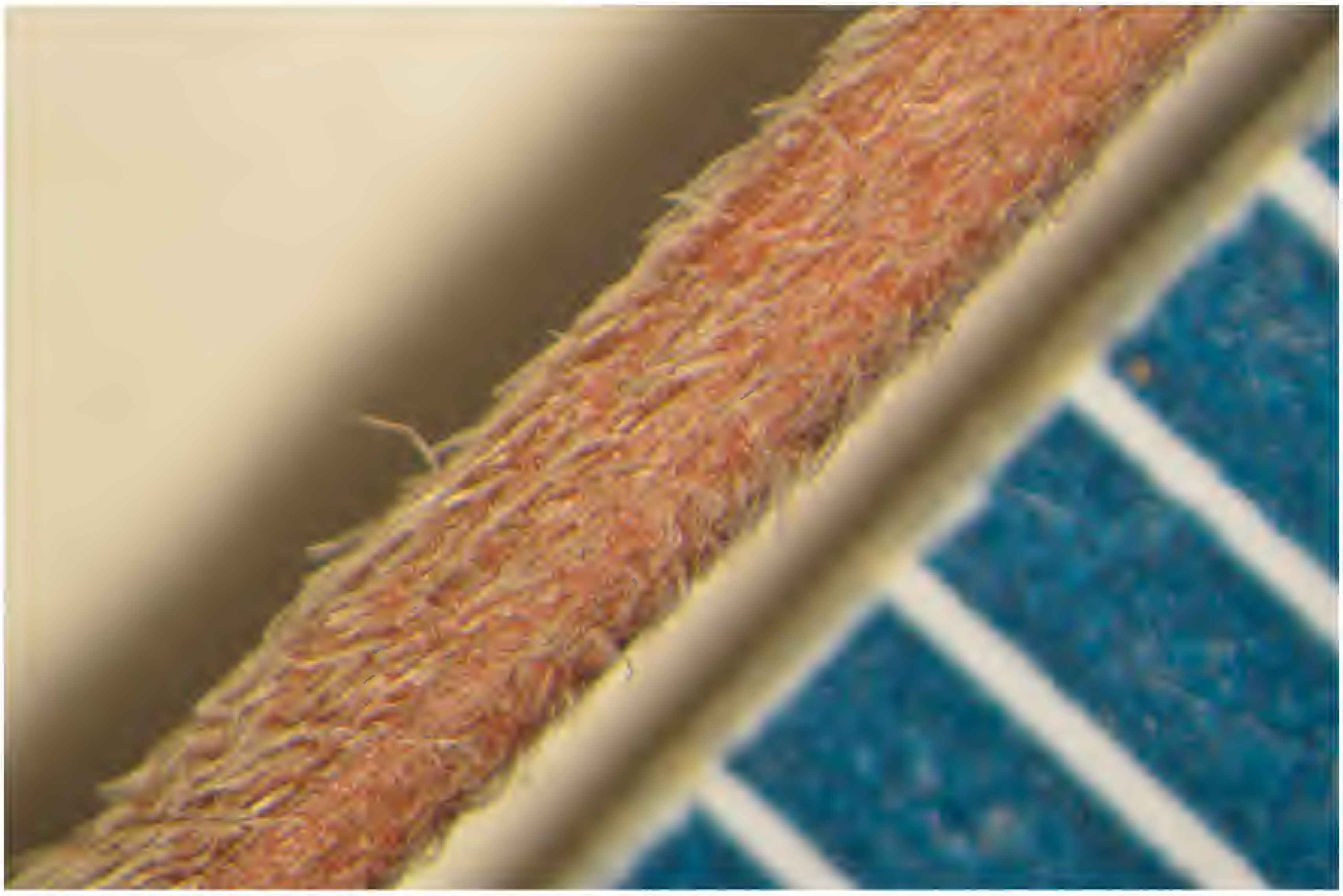


Figure 16. *Galactia michauxii*, with a retrorsely strigose stem (*Lakela 24958*). The distal portion of the stem is towards the upper right.

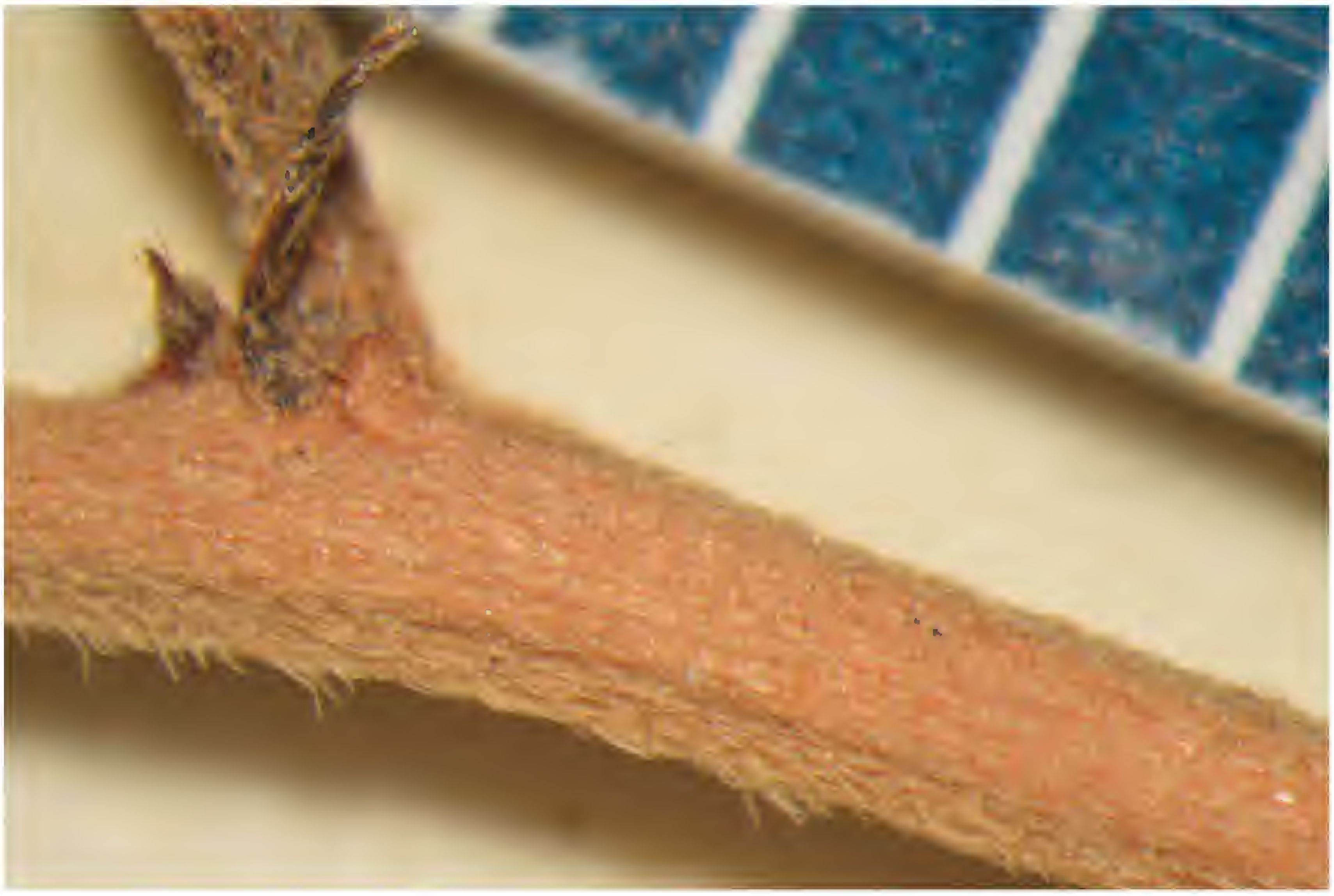


Figure 17. *Galactia michauxii*, with a retrorsely strigose stem and petiole in the upper left (*Seymour 91 7 20* [19126]). The distal portion of the stem is towards the left.

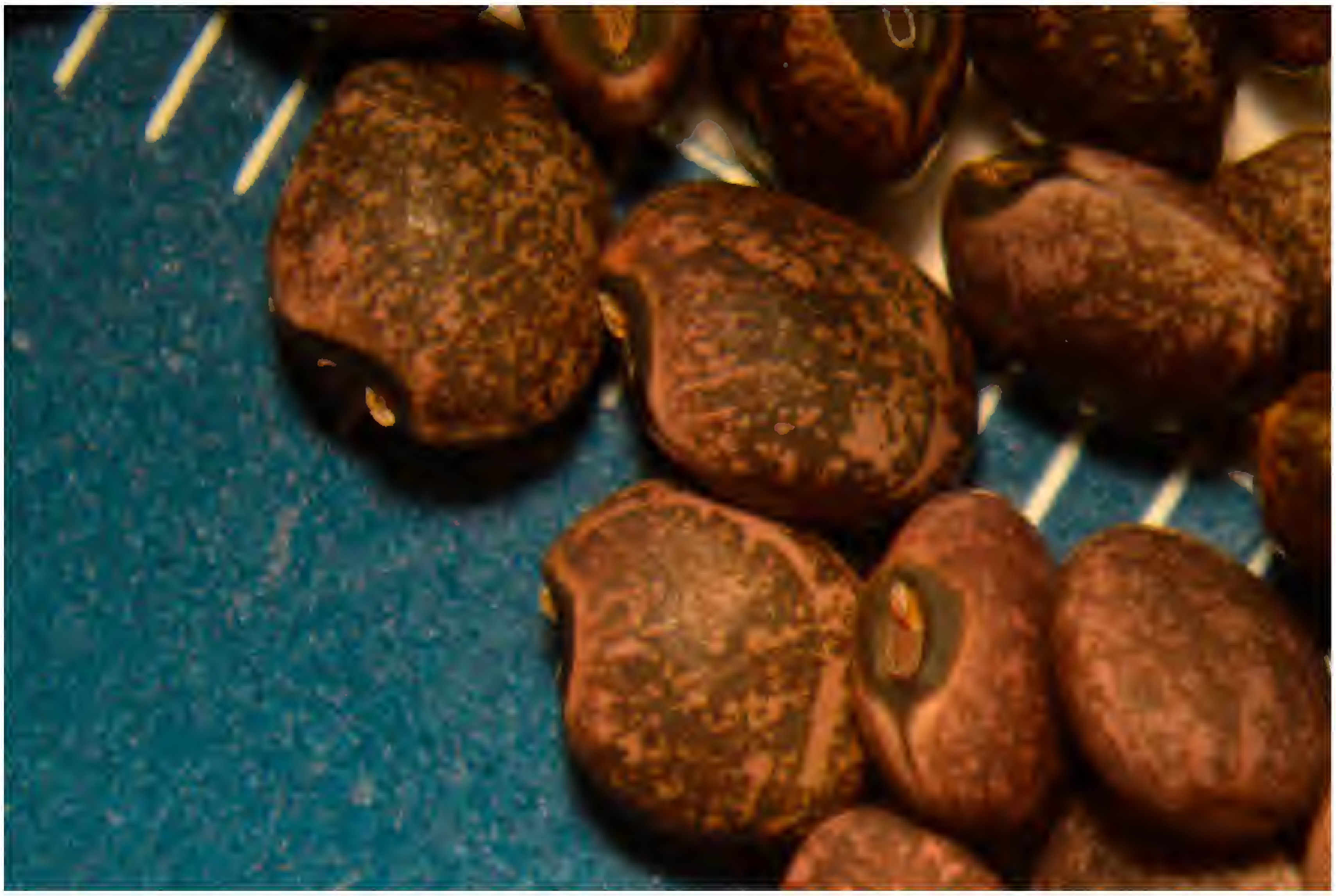


Figure 18. *Galactia michauxii*, seeds (*Franck 1478*).

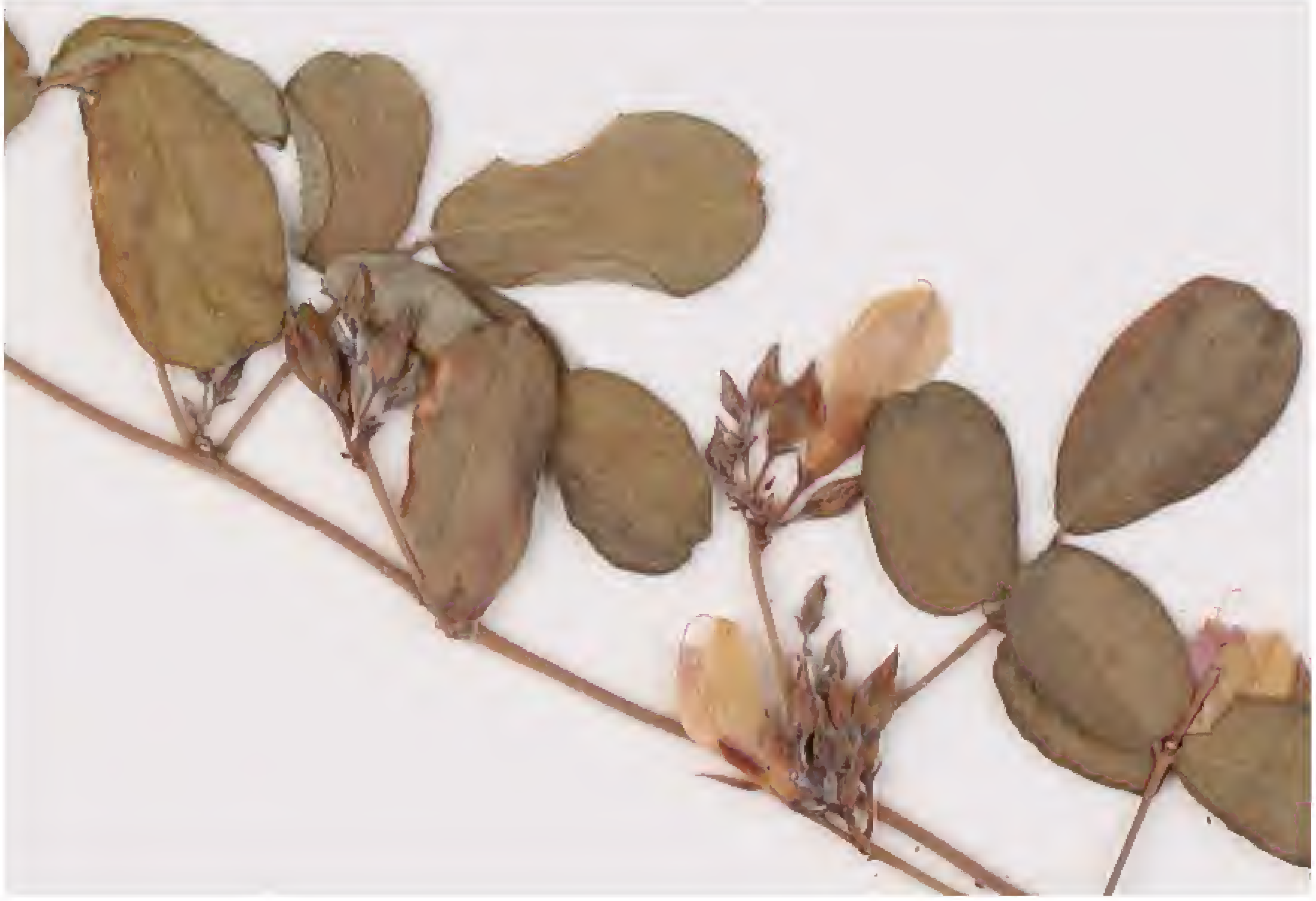


Figure 19. *Galactia microphylla* (*Carlton s.n.* [162778]).

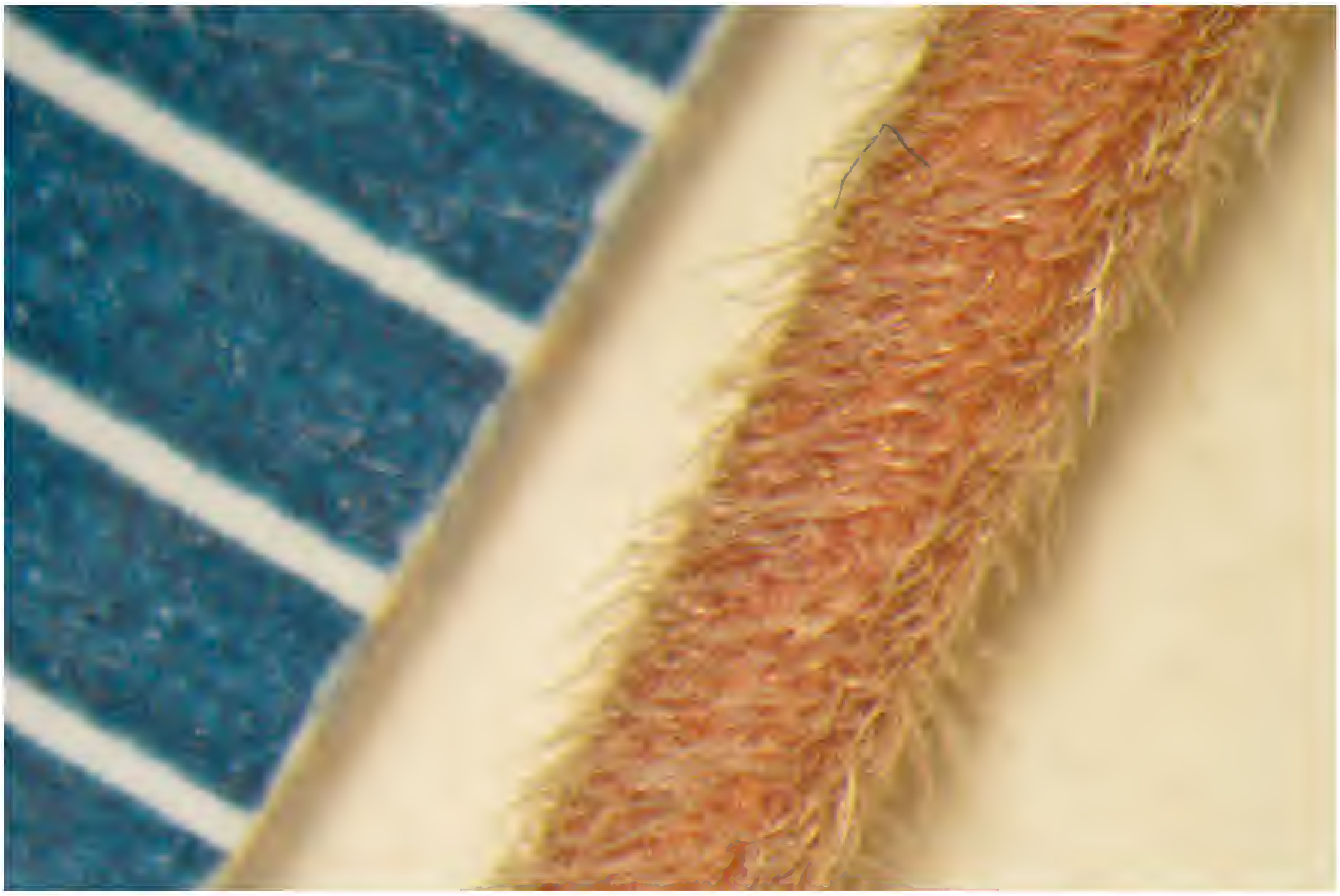


Figure 20. *Galactia microphylla*, with a retrorsely villous stem (*Carlton s.n.* [acc. no. 162778]). The distal portion of the stem is towards the upper right.

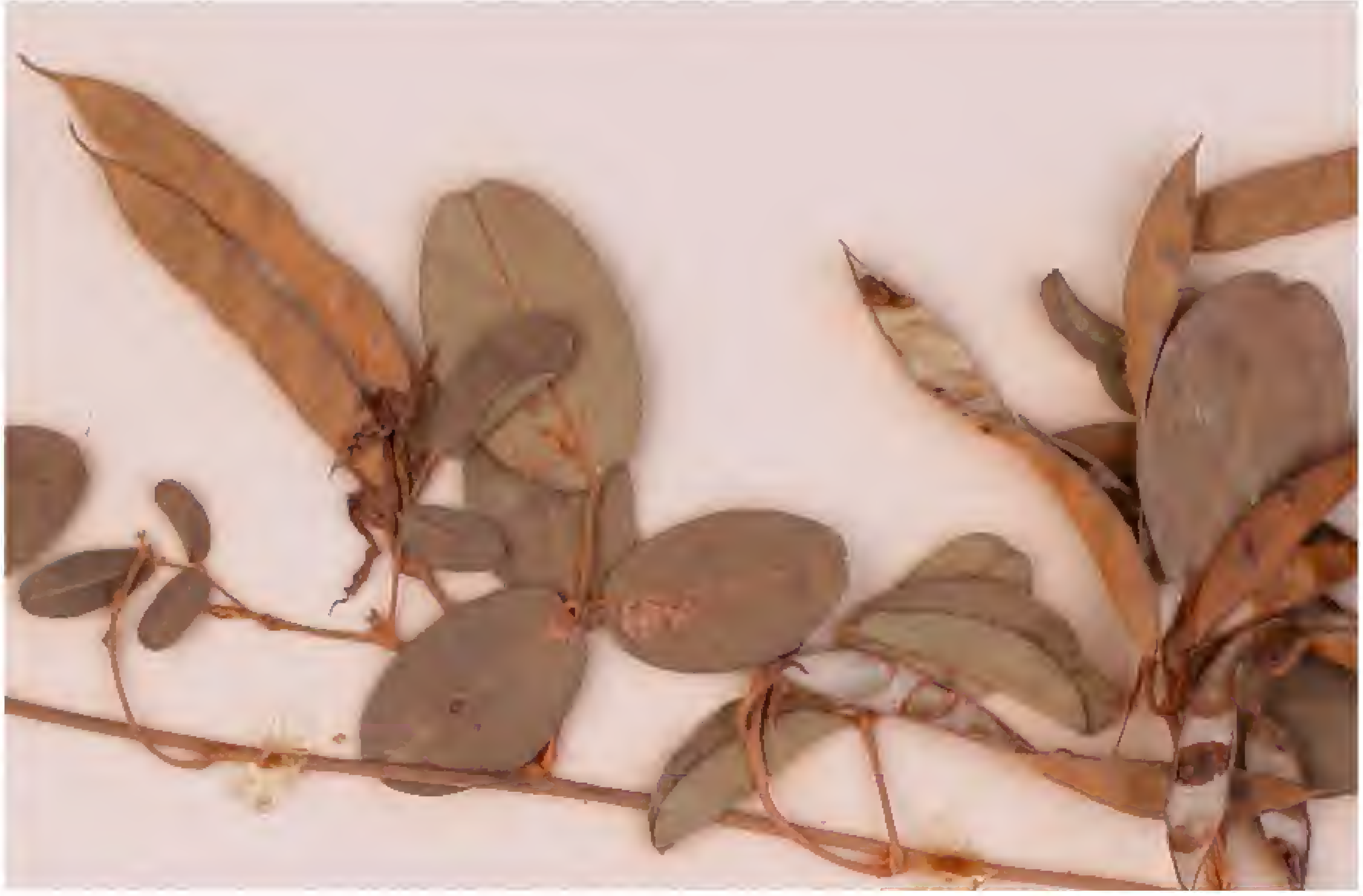


Figure 21. *Galactia minor* (*Kral & Godfrey 6064*).

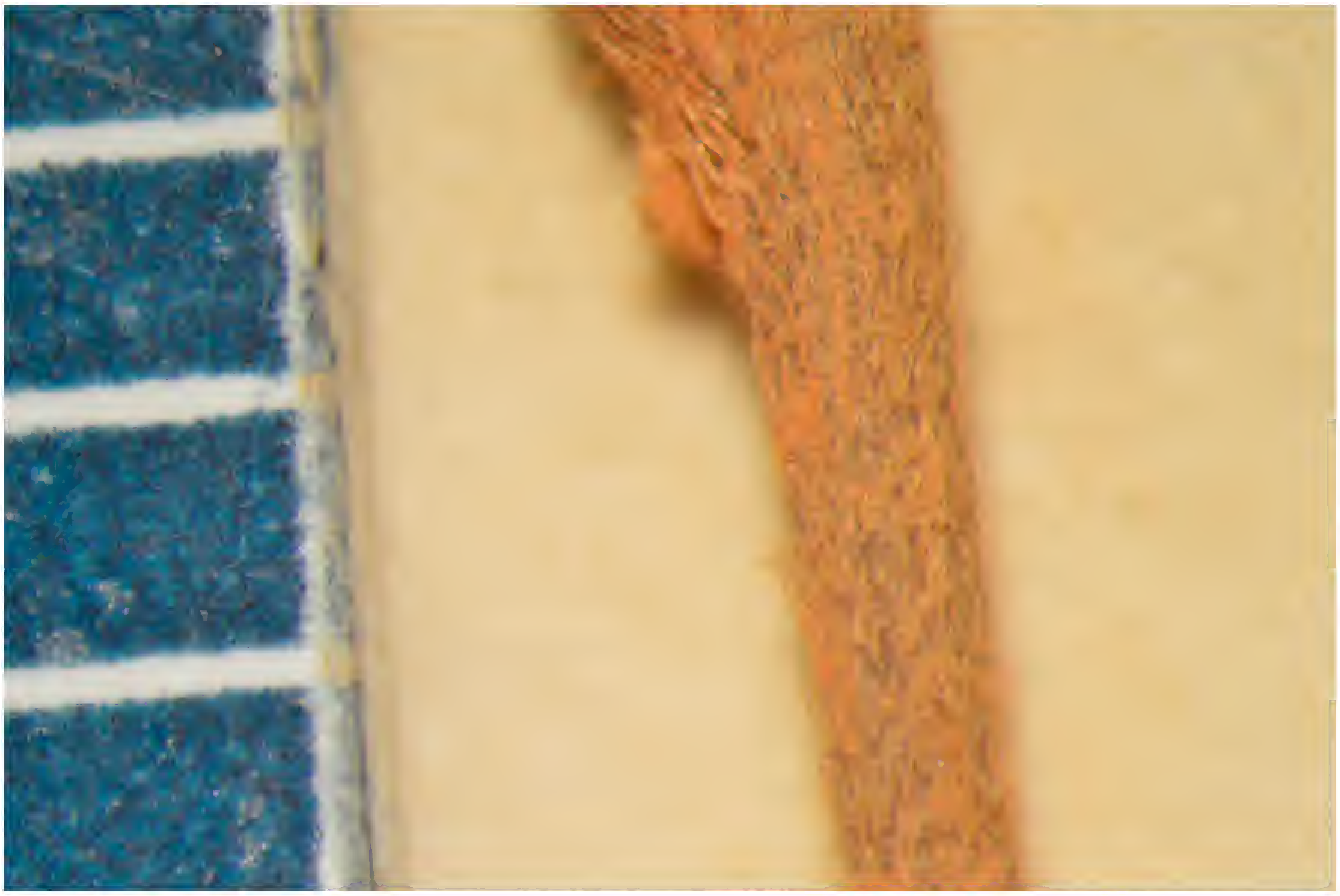


Figure 22. *Galactia minor*, with an antrorsely strigose stem (*Kral & Godfrey 6064*). The distal portion of the stem is towards the top.

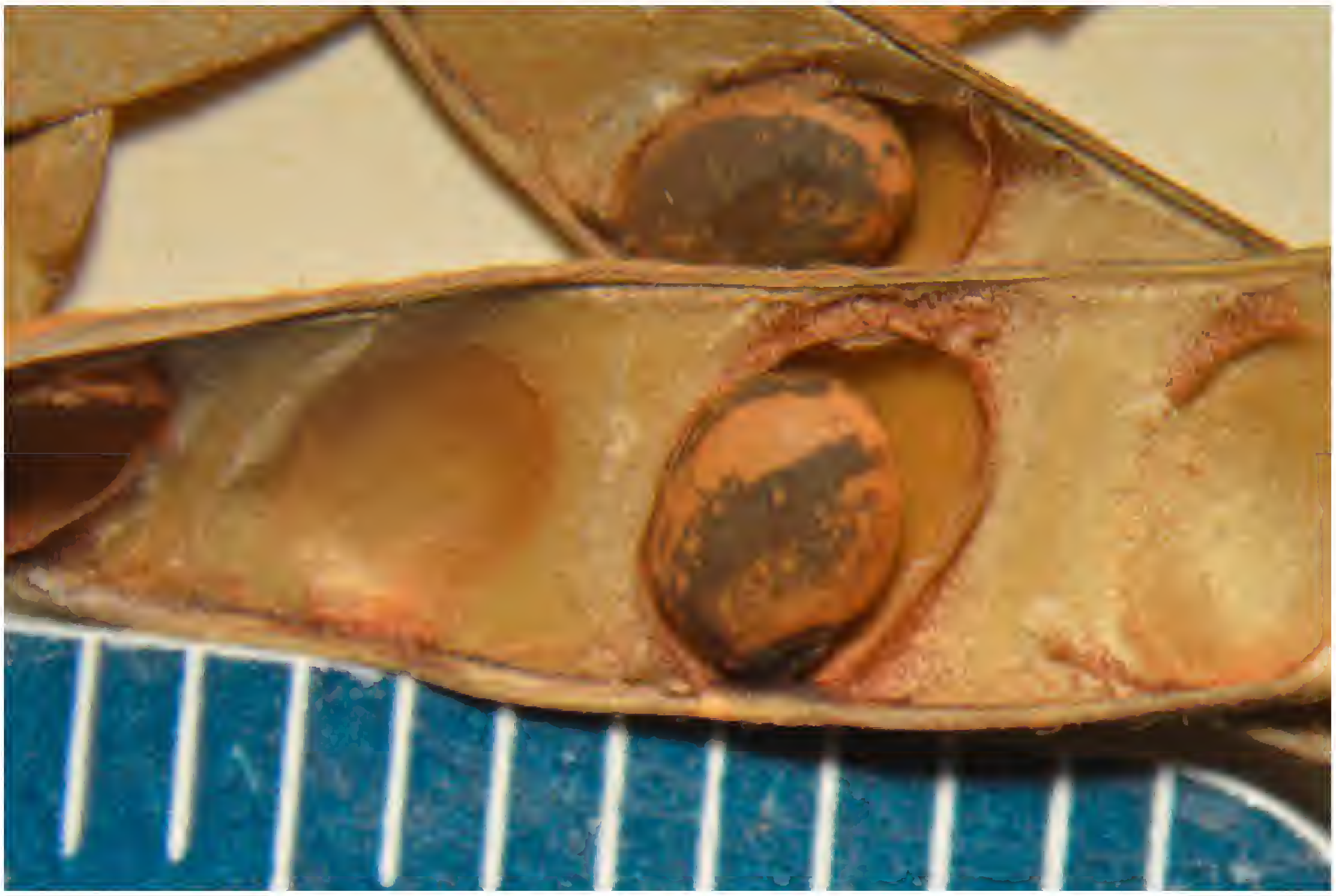


Figure 23. *Galactia minor*, seeds attached to the fruit. (*Kral & Godfrey 6064*).

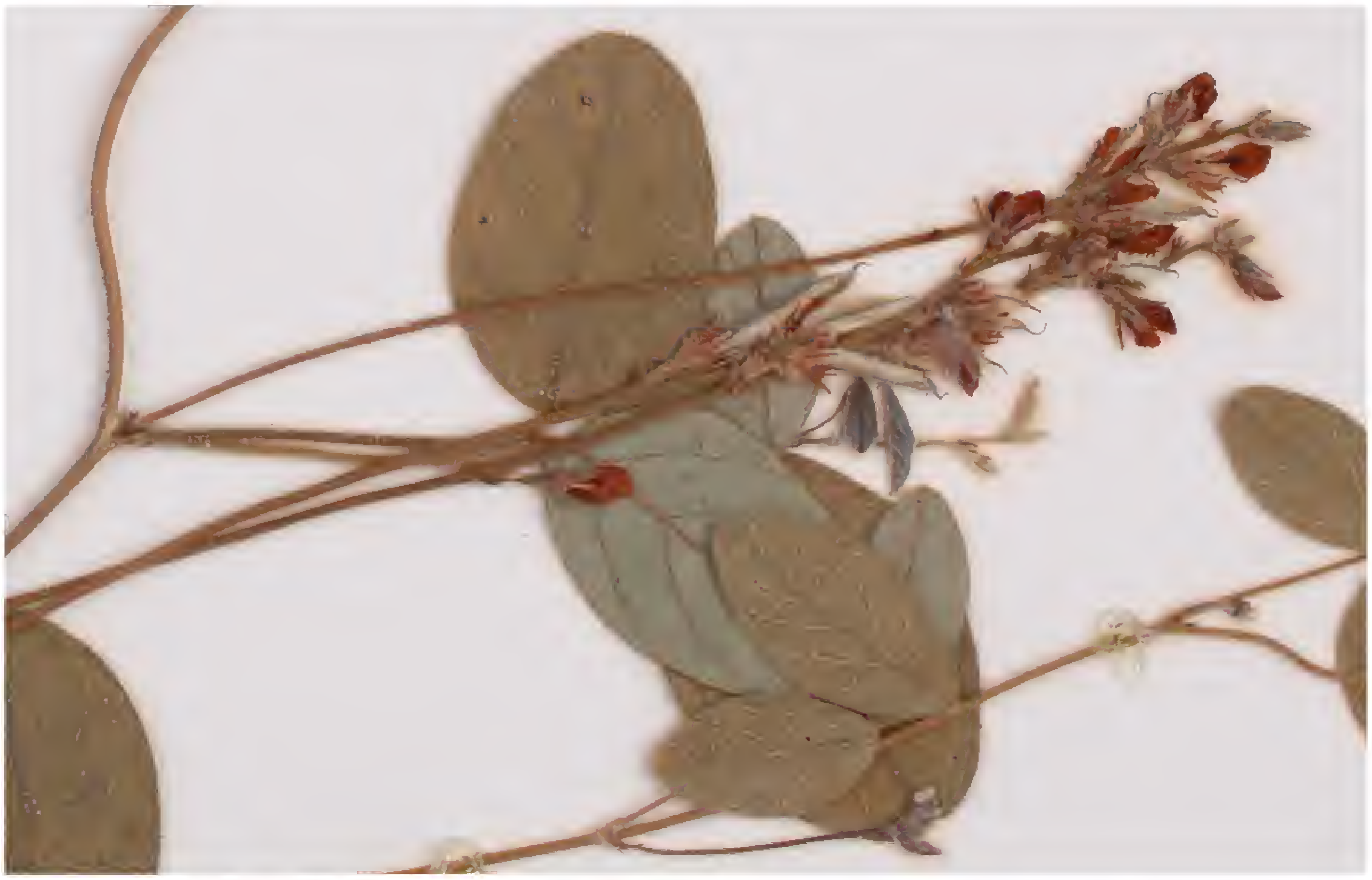


Figure 24. *Galactia mollis* (*Ahles & Haesloop 29747*).

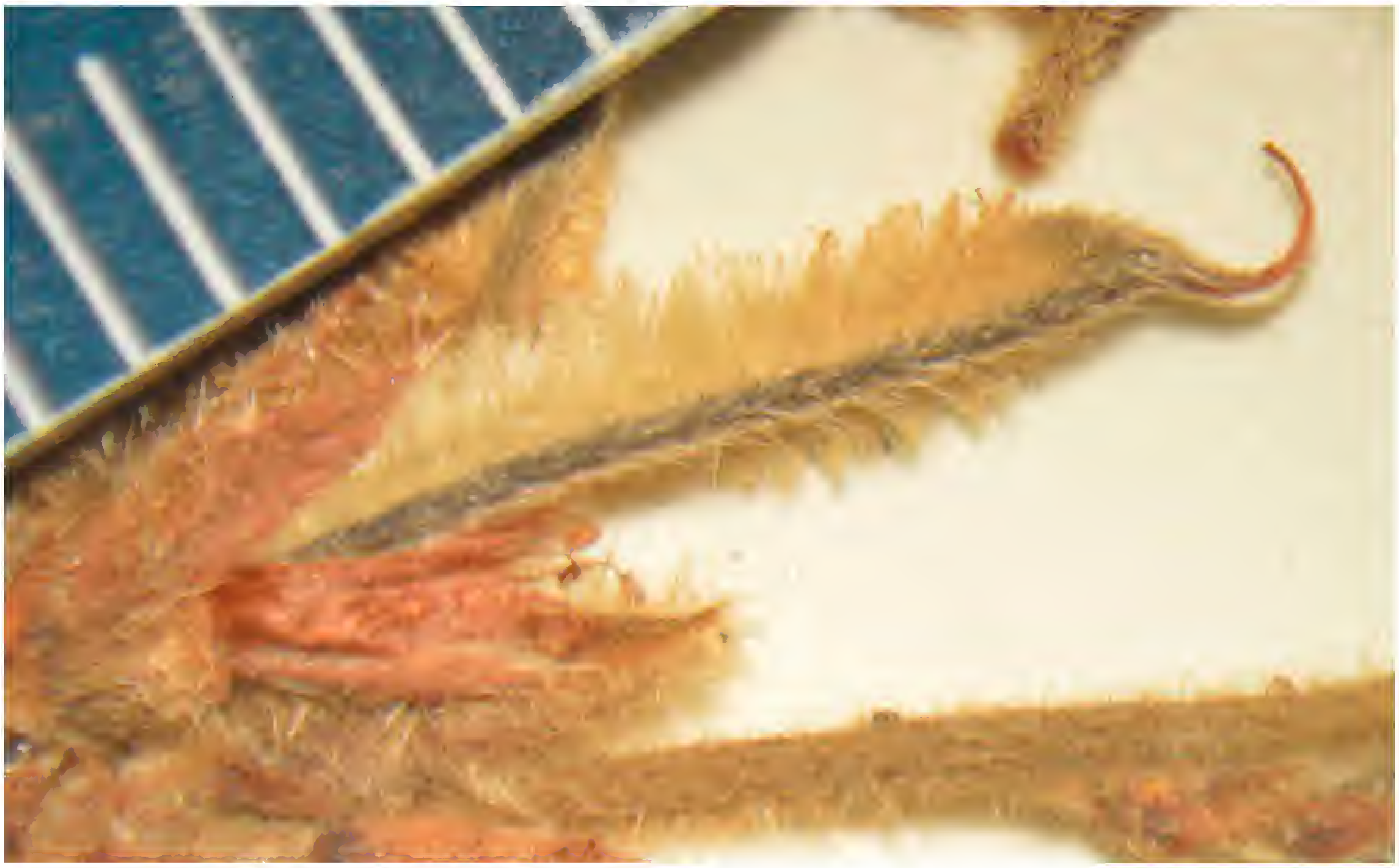


Figure 25. *Galactia mollis*, with a spreading villous immature fruit, and persistent reddish stamens and calyx (*Daubenmire & Daubenmire s.n.* [179710]). The distal portion of the inflorescence is towards the right.

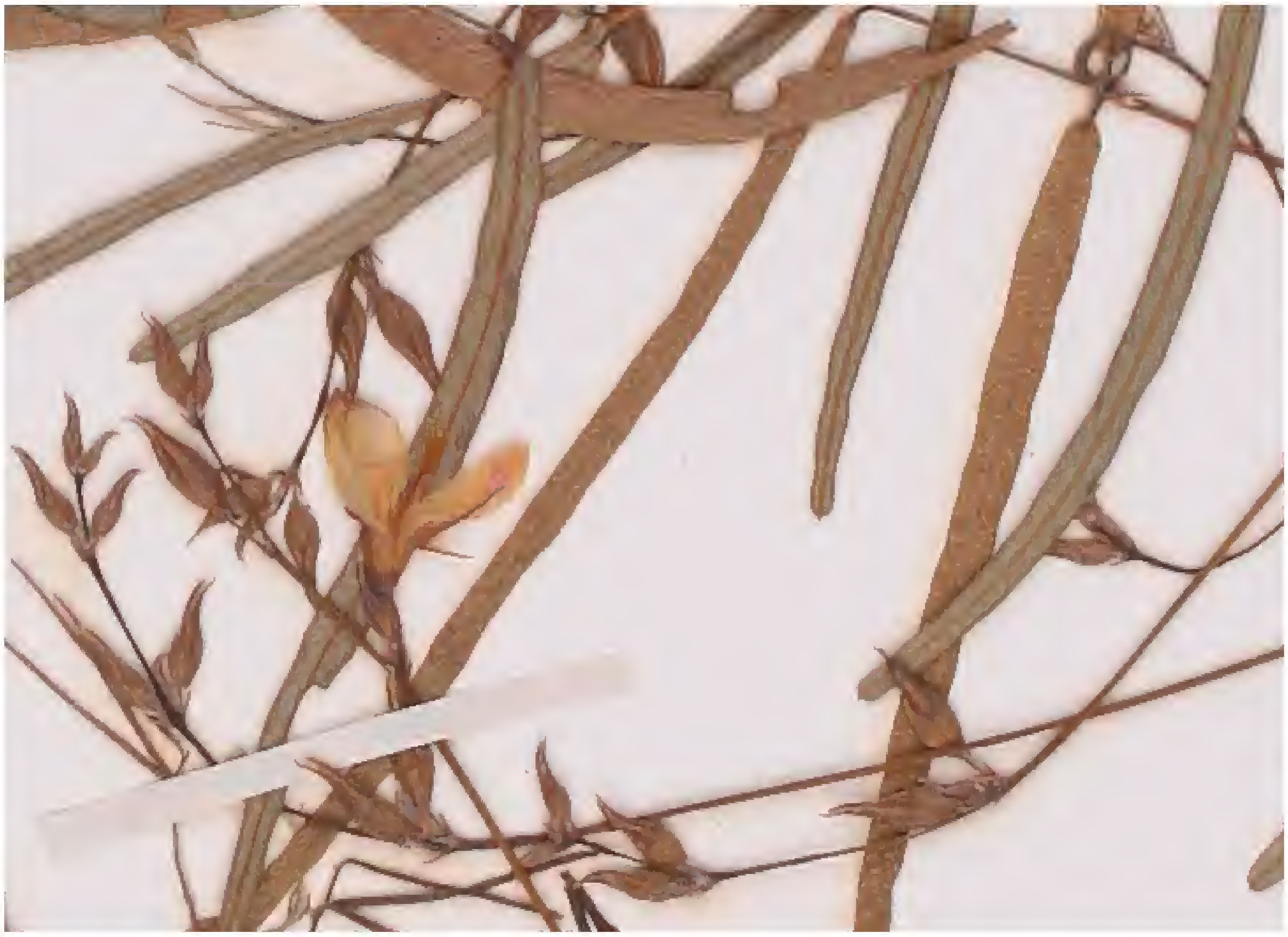


Figure 26. *Galactia pinetorum* (*Britton s.n.* [192046]).

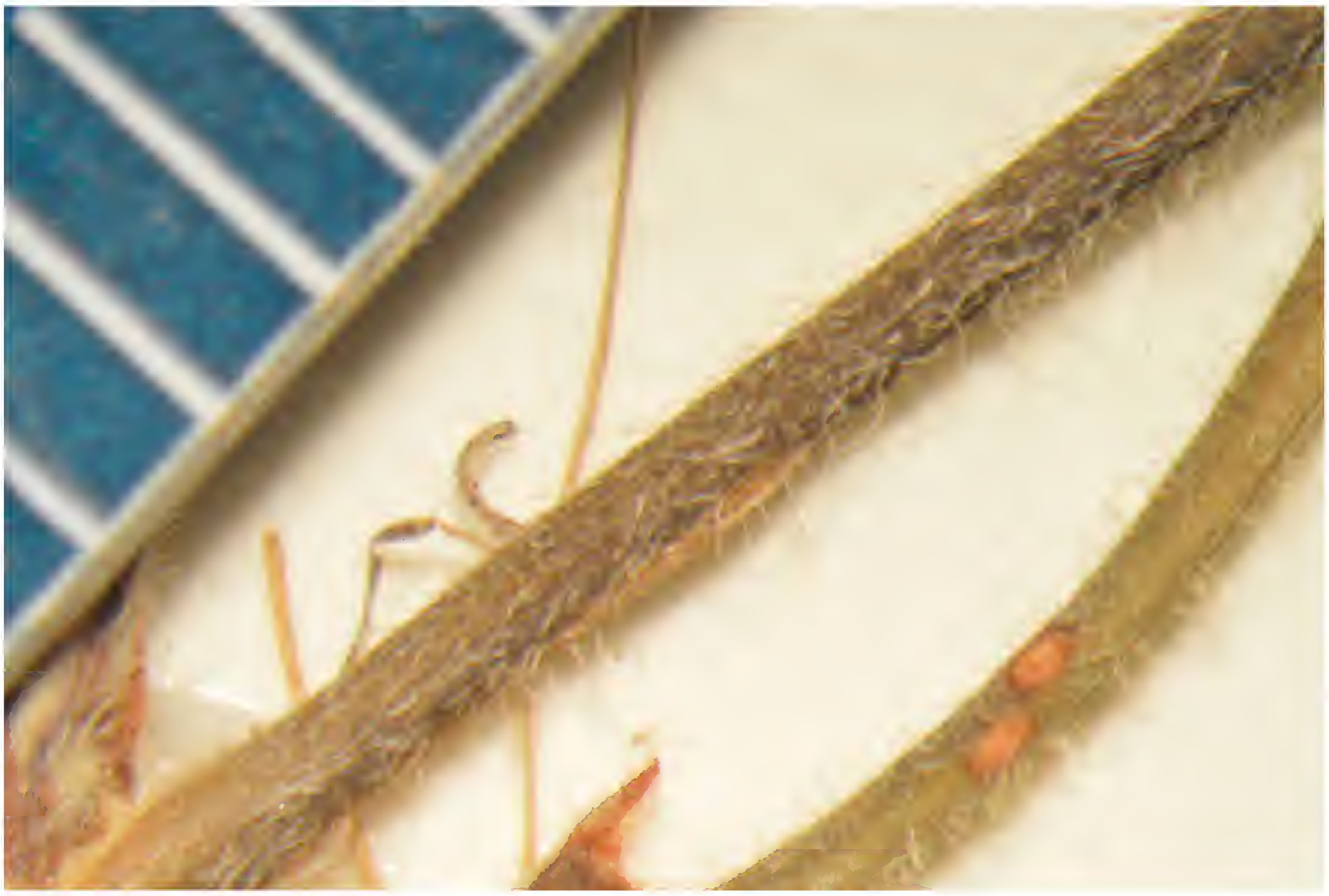


Figure 27. *Galactia pinetorum*, with a retrorsely pilose stem and an inflorescence rachis on the right (*Bradley 1670*). The distal portion of the stem is towards the the upper right.

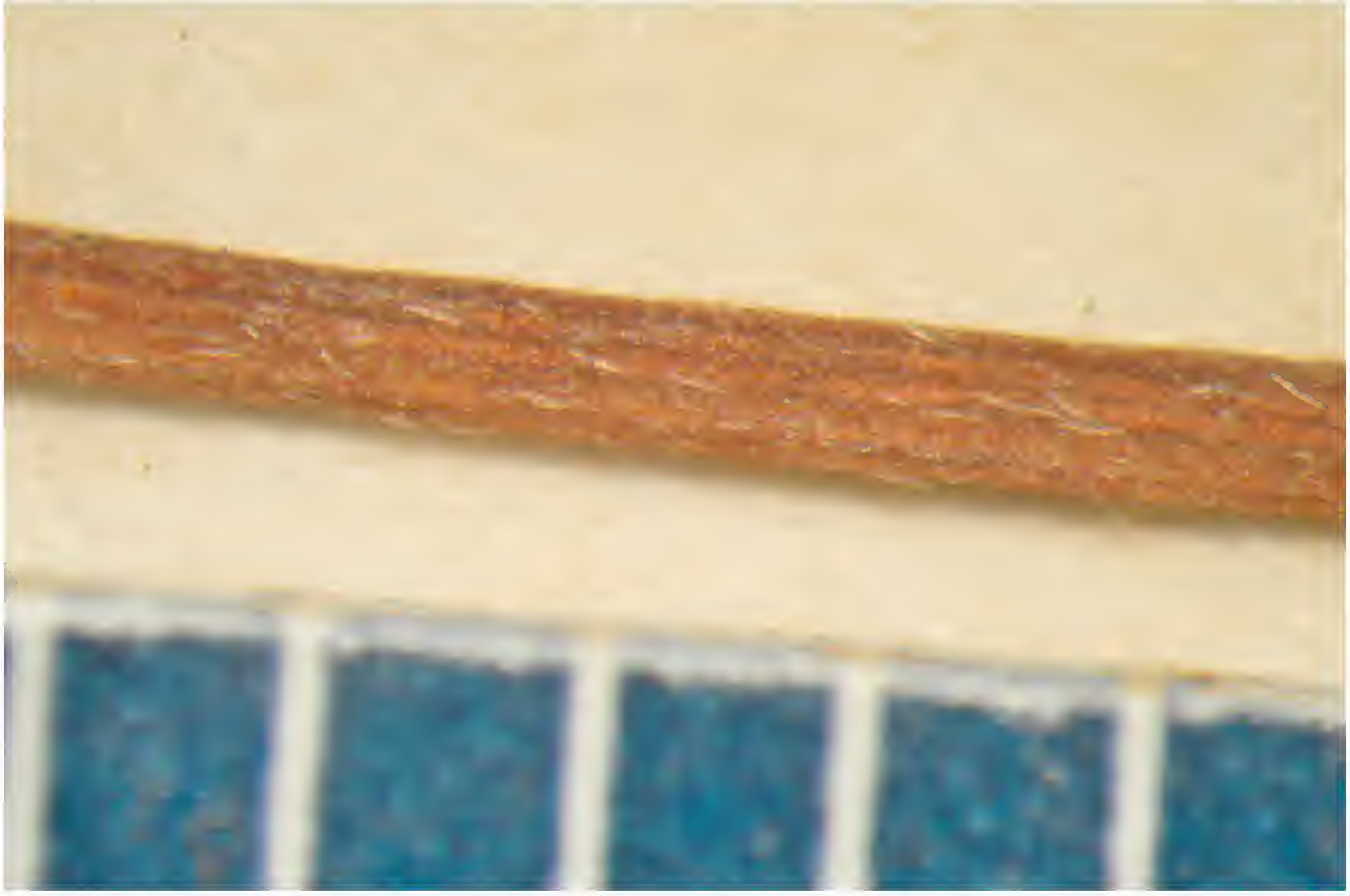


Figure 28. *Galactia pinetorum*, with a retrorsely sparsely strigose stem (*Broome s.n.* [75282]). The distal portion of the stem is towards the left.

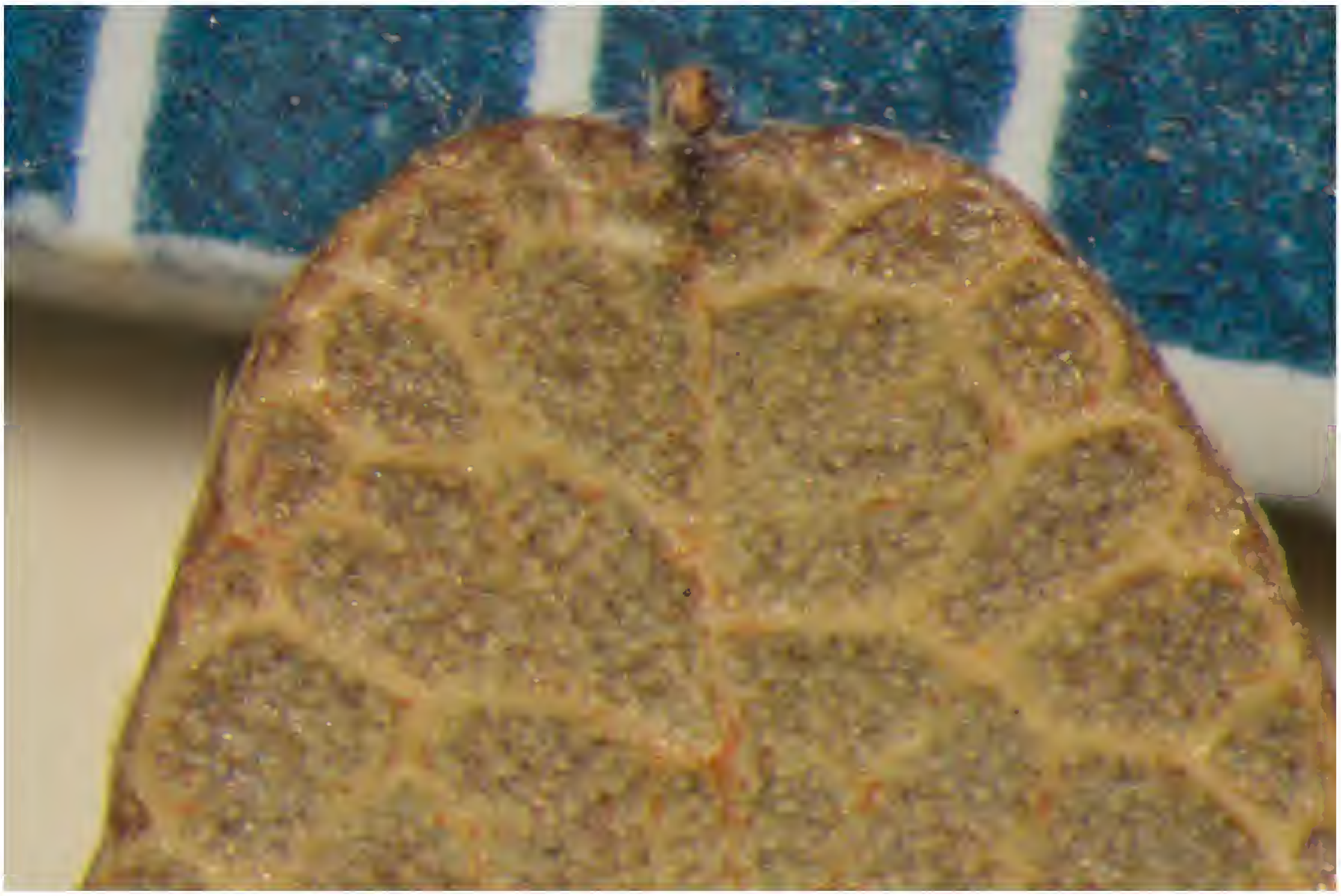


Figure 29. *Galactia pinetorum*, with pellucid dots throughout the adaxial surface of the leaflet (*Lakela 28773*).

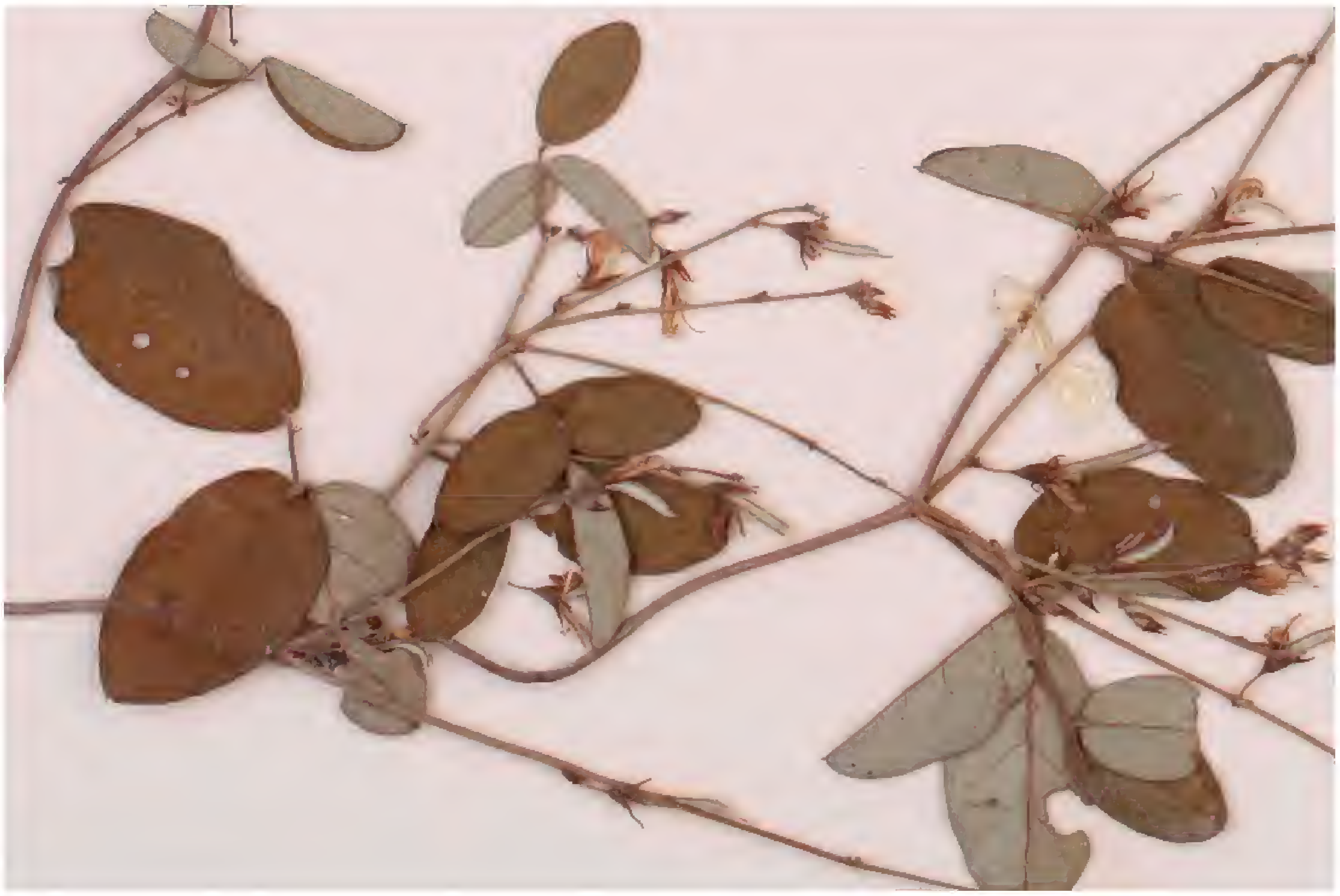


Figure 30. *Galactia regularis* (*Wharton 5705*).

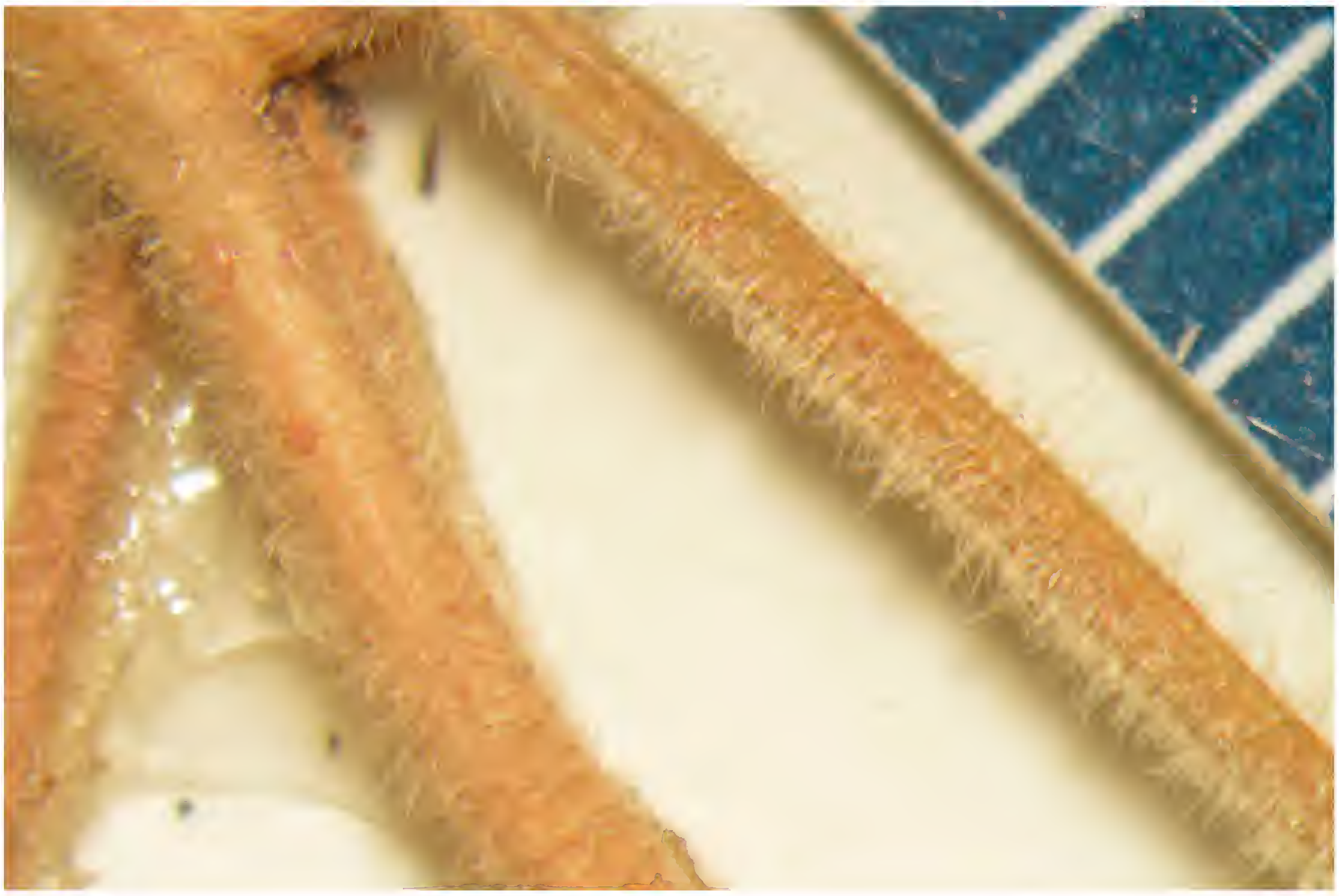


Figure 31. *Galactia regularis*, with villous stems (middle, right) and a petiole (left) (*Duncan 17183*). The distal portion of the middle stem is towards the bottom and of the right stem towards the top.

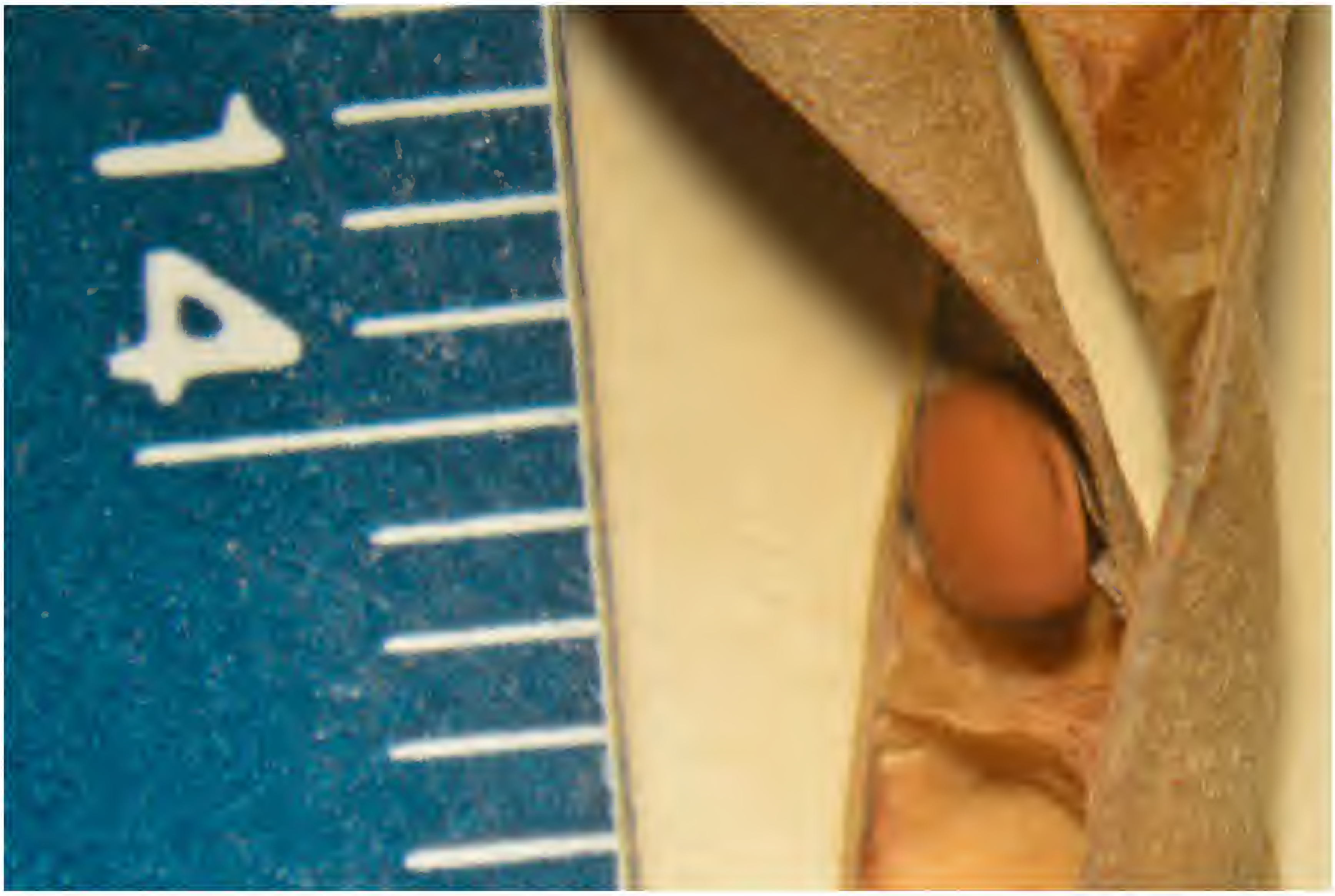


Figure 32. *Galactia regluaris*, likely an immature seed attached to the fruit (*Seymour 49* [19358]).

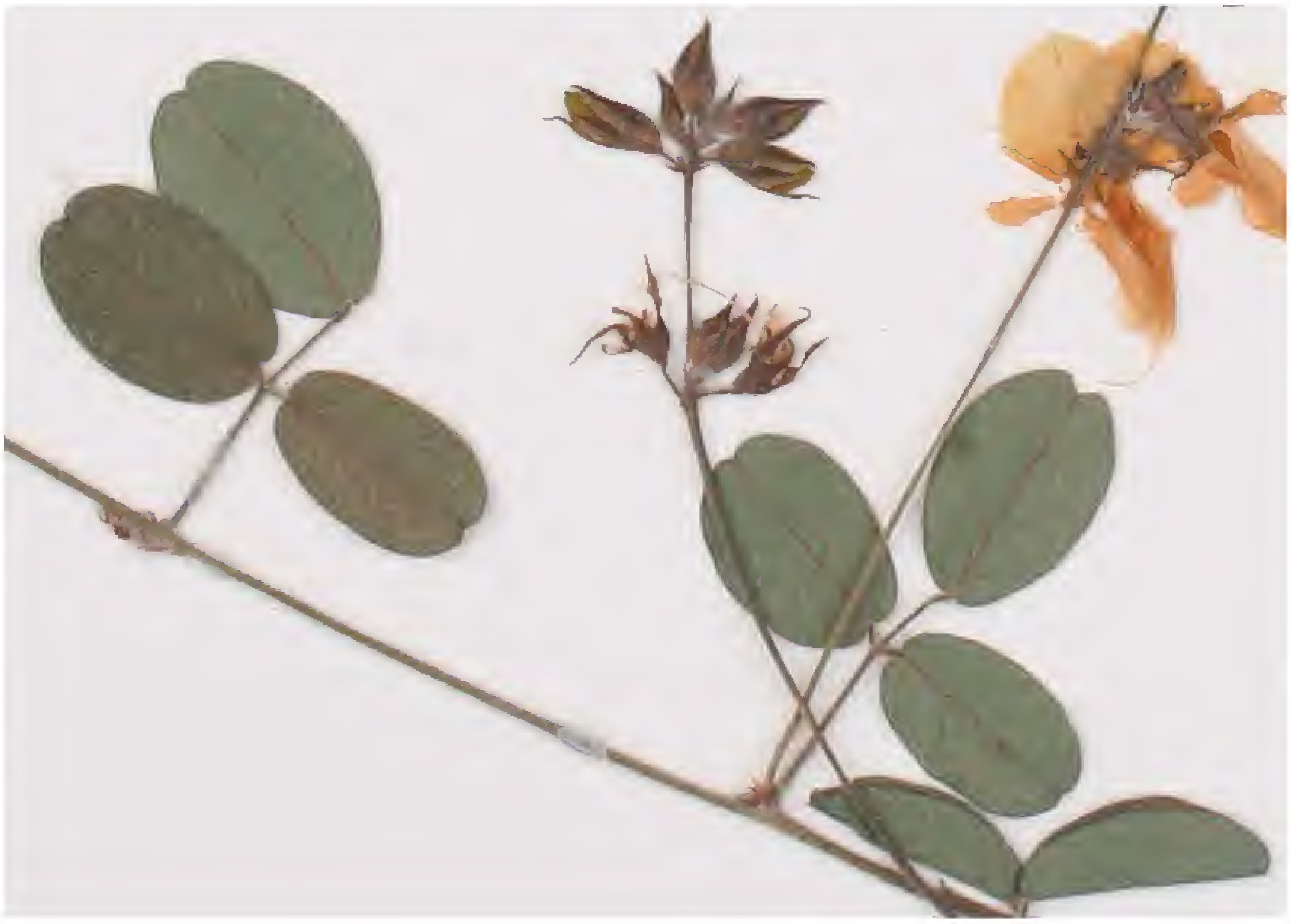


Figure 33. *Galactia smallii* (*Woodmansee & Hoffman 30*).

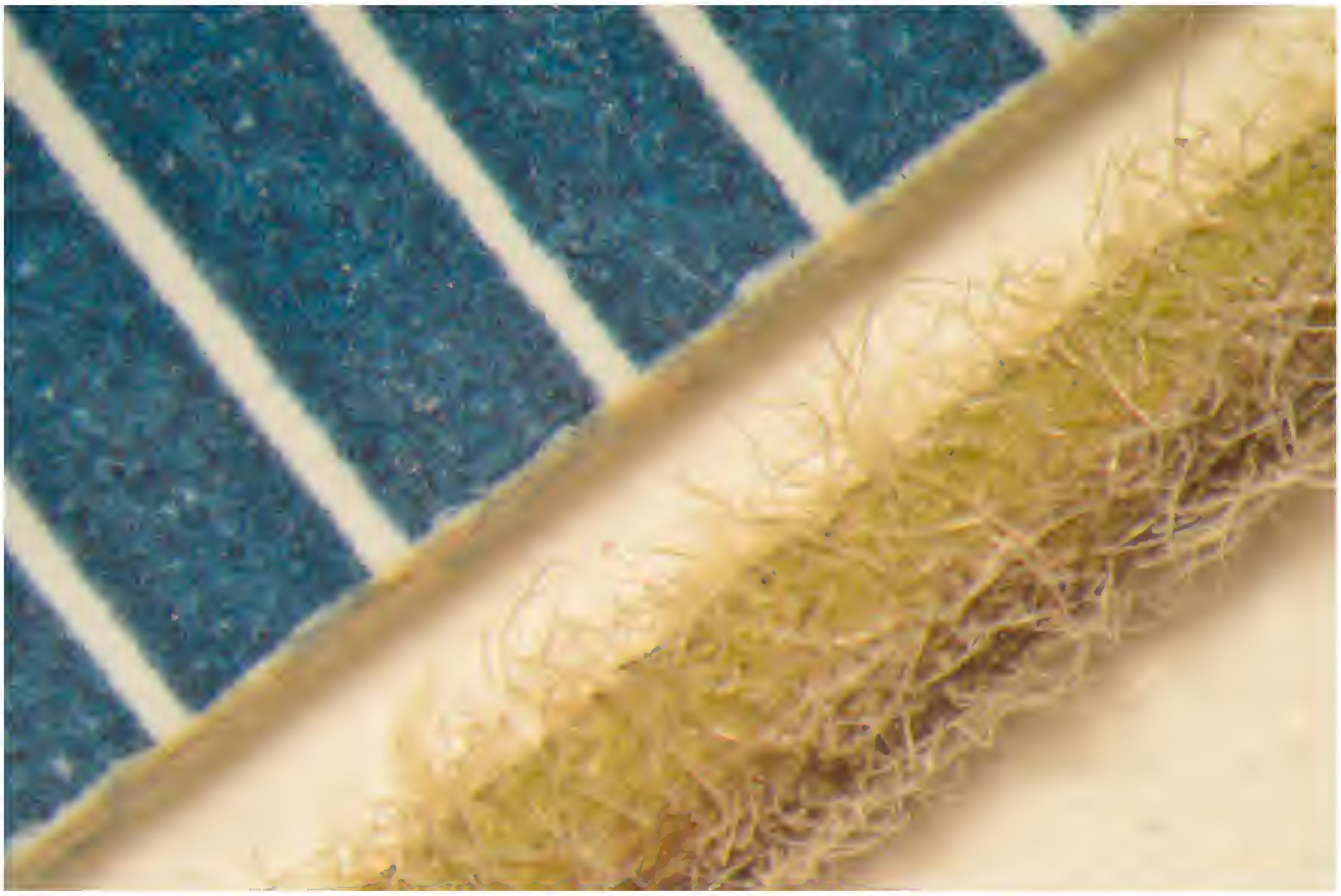


Figure 34. *Galactia smallii*, with a villous stem (*Franck 3923*). The distal portion of the stem is towards the right.

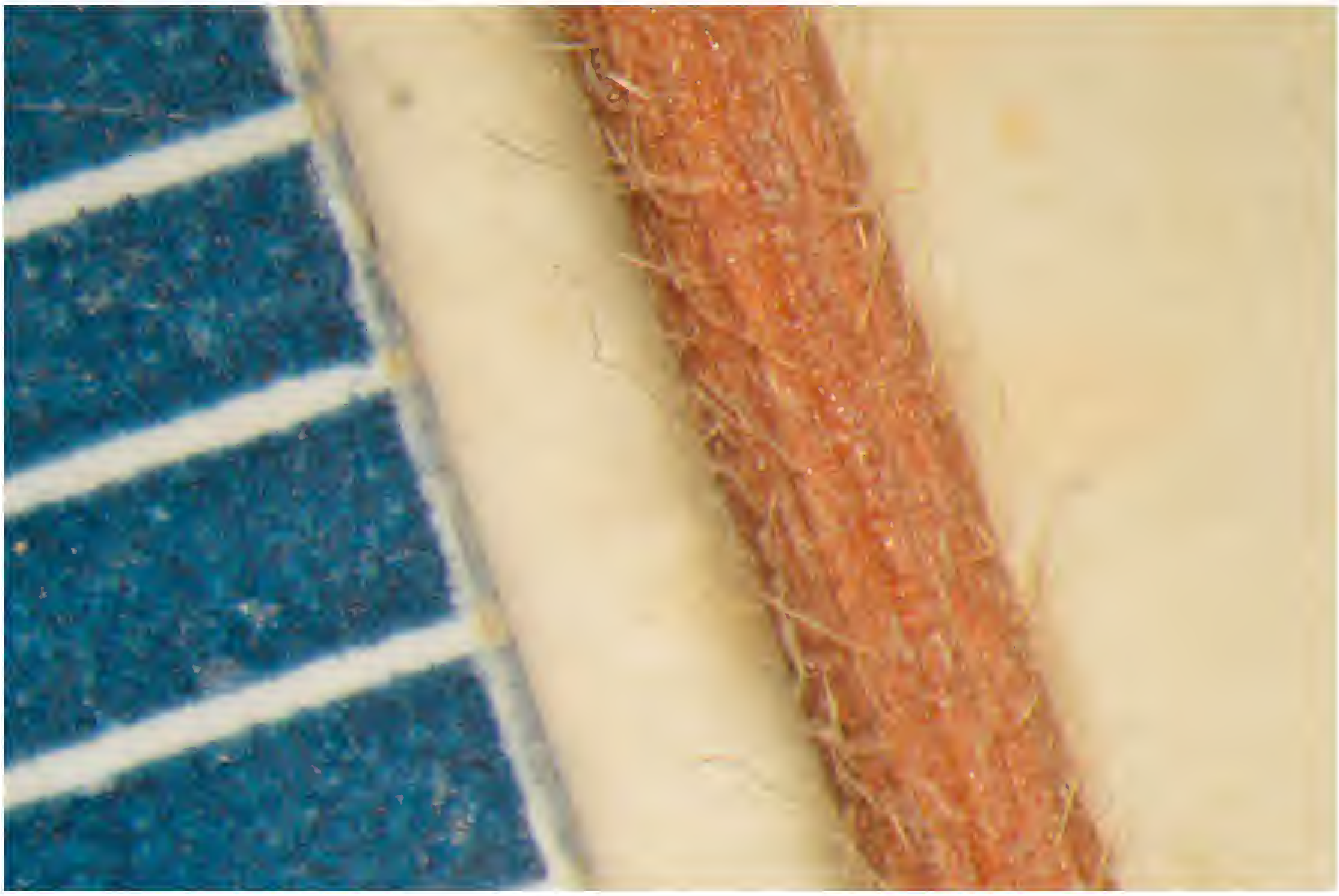


Figure 35. *Galactia smallii*, with an antrorsely pilose stem (*Lakela 28766*). The distal portion of the stem is towards the top.

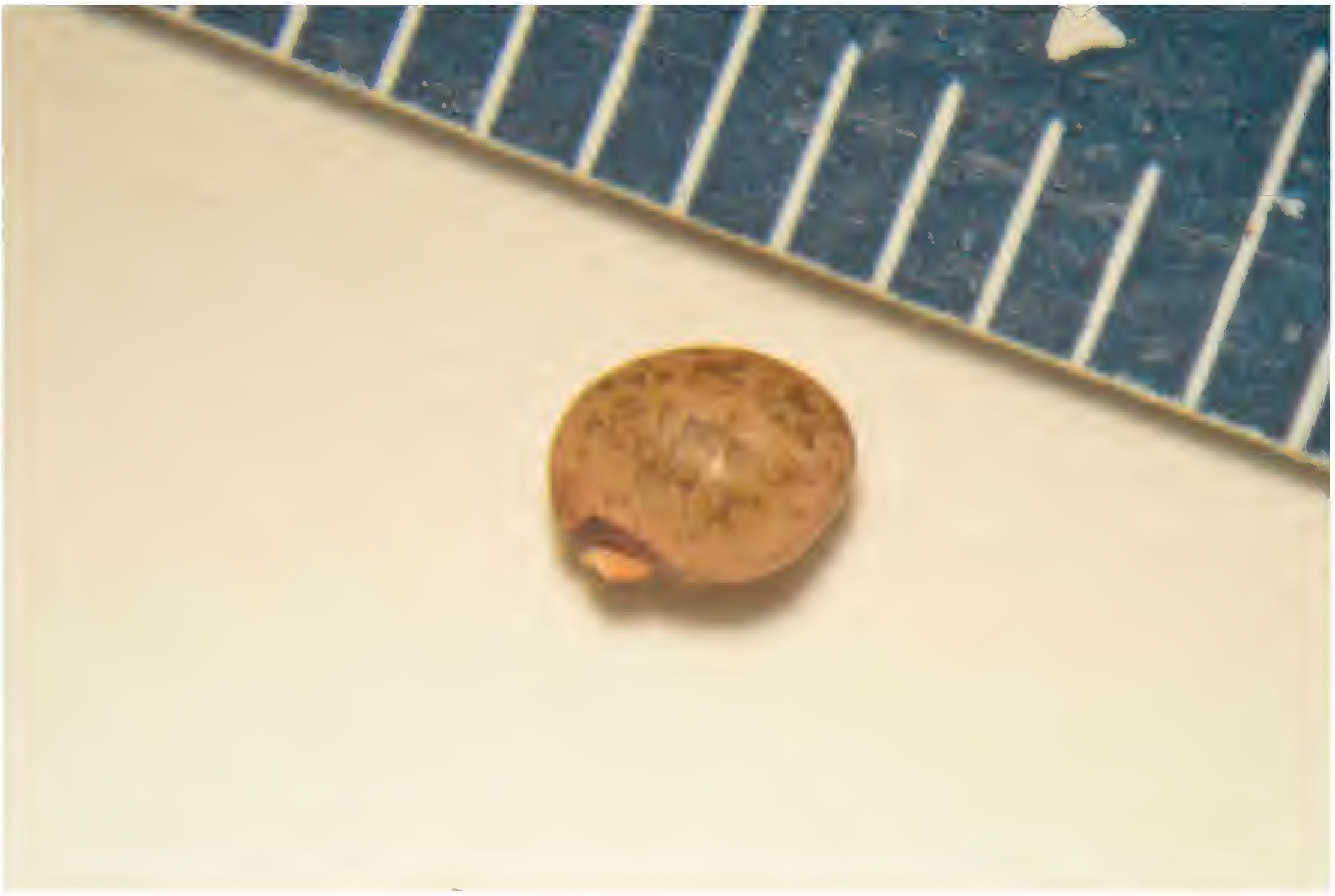


Figure 36. *Galactia smallii*, seed, possibly immature (*Franck 3923*).

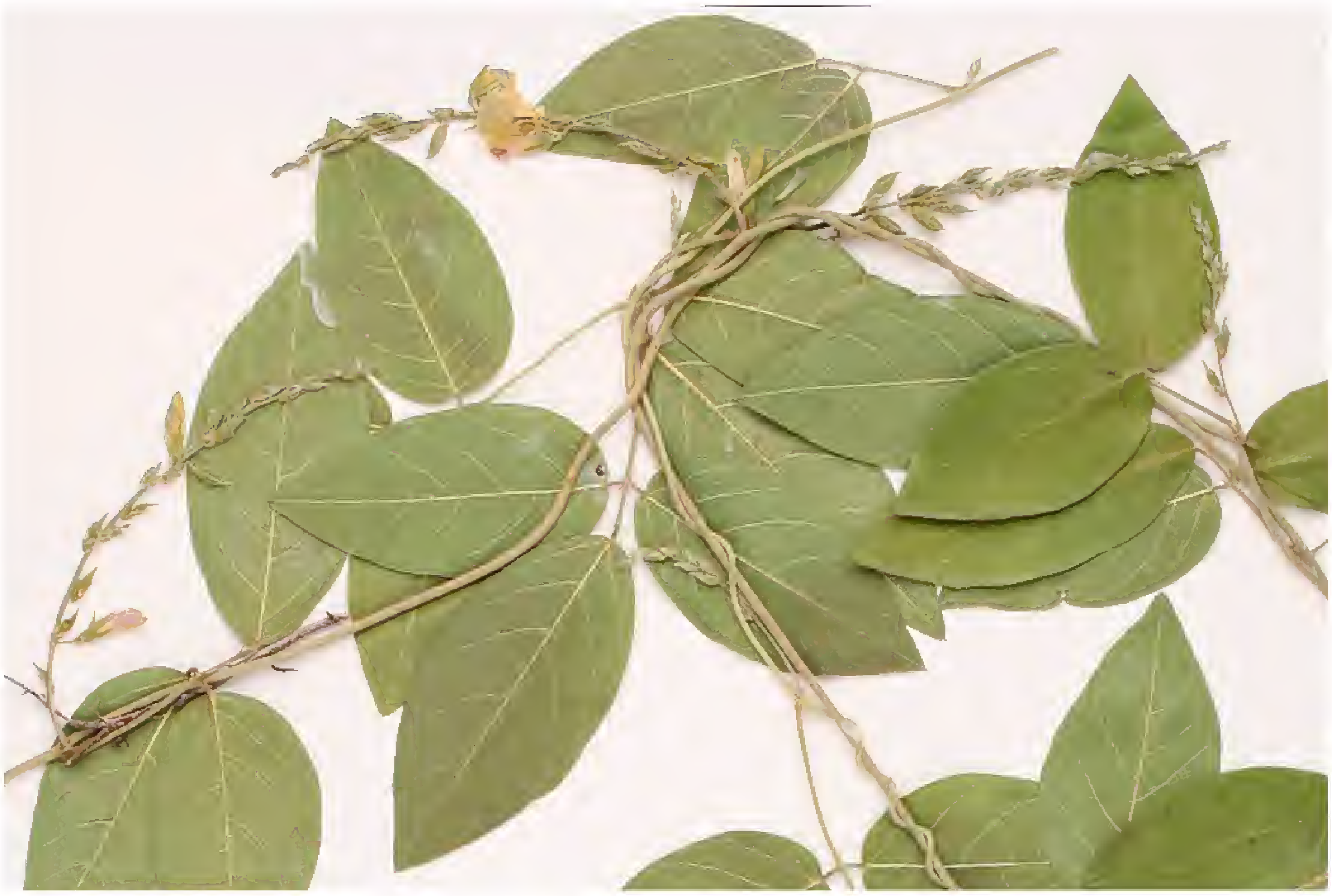


Figure 37. *Galactia striata* (*Longbottom & Williams 5465*).

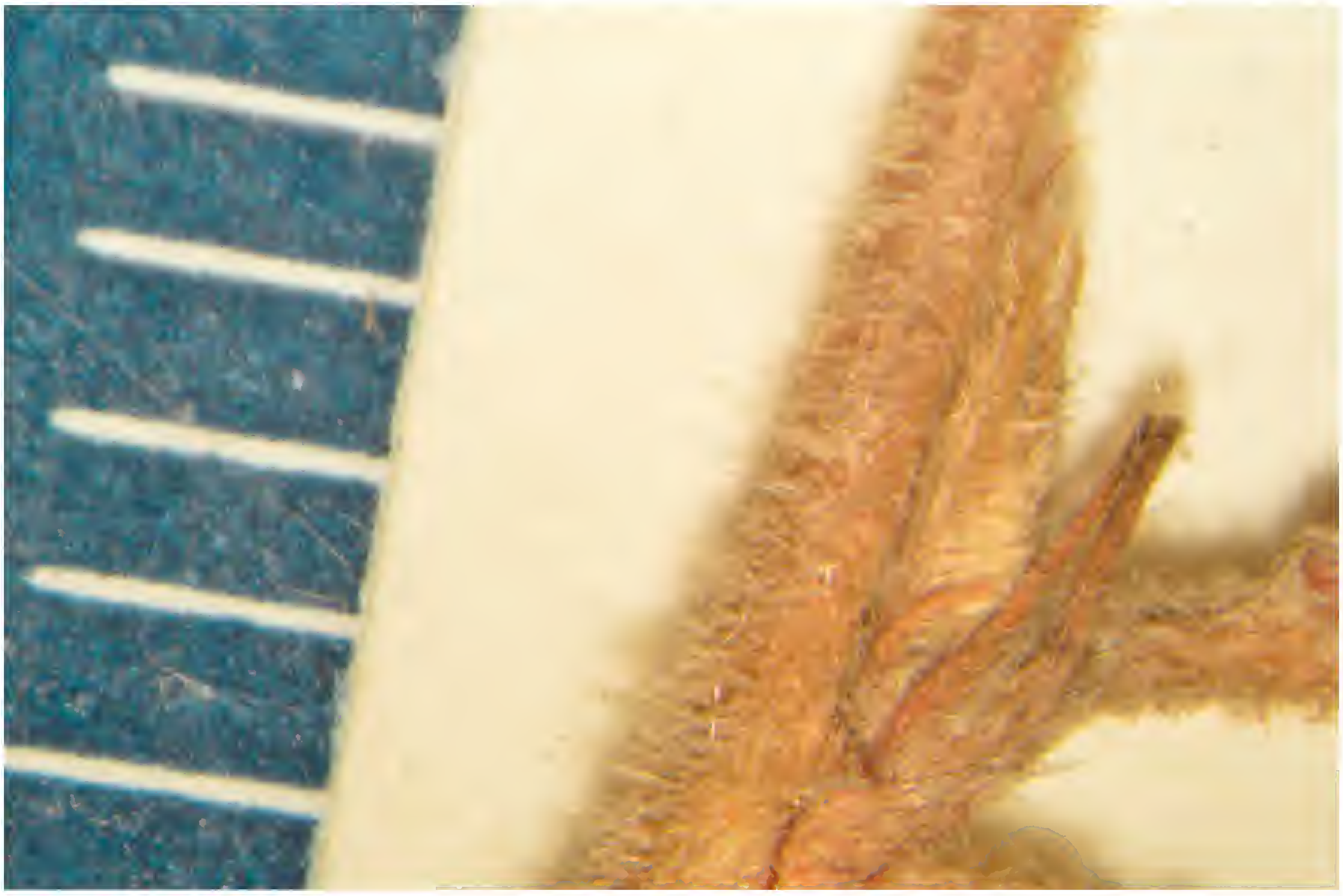


Figure 38. *Galactia striata*, with a villous stem (*Todd 91*). The distal portion of the stem is towards the top.

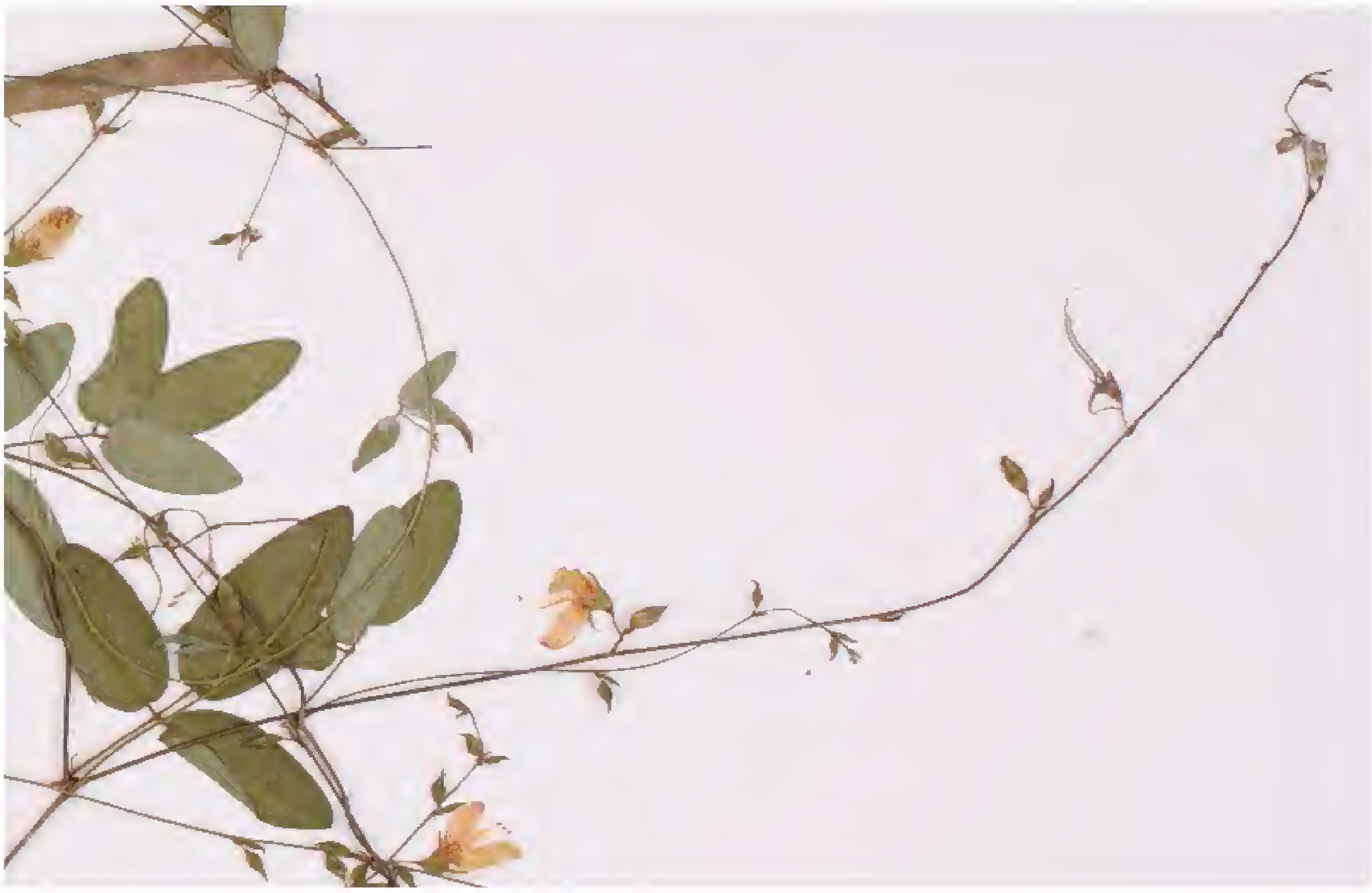


Figure 39. *Galactia volubilis* (*Franck 868*).

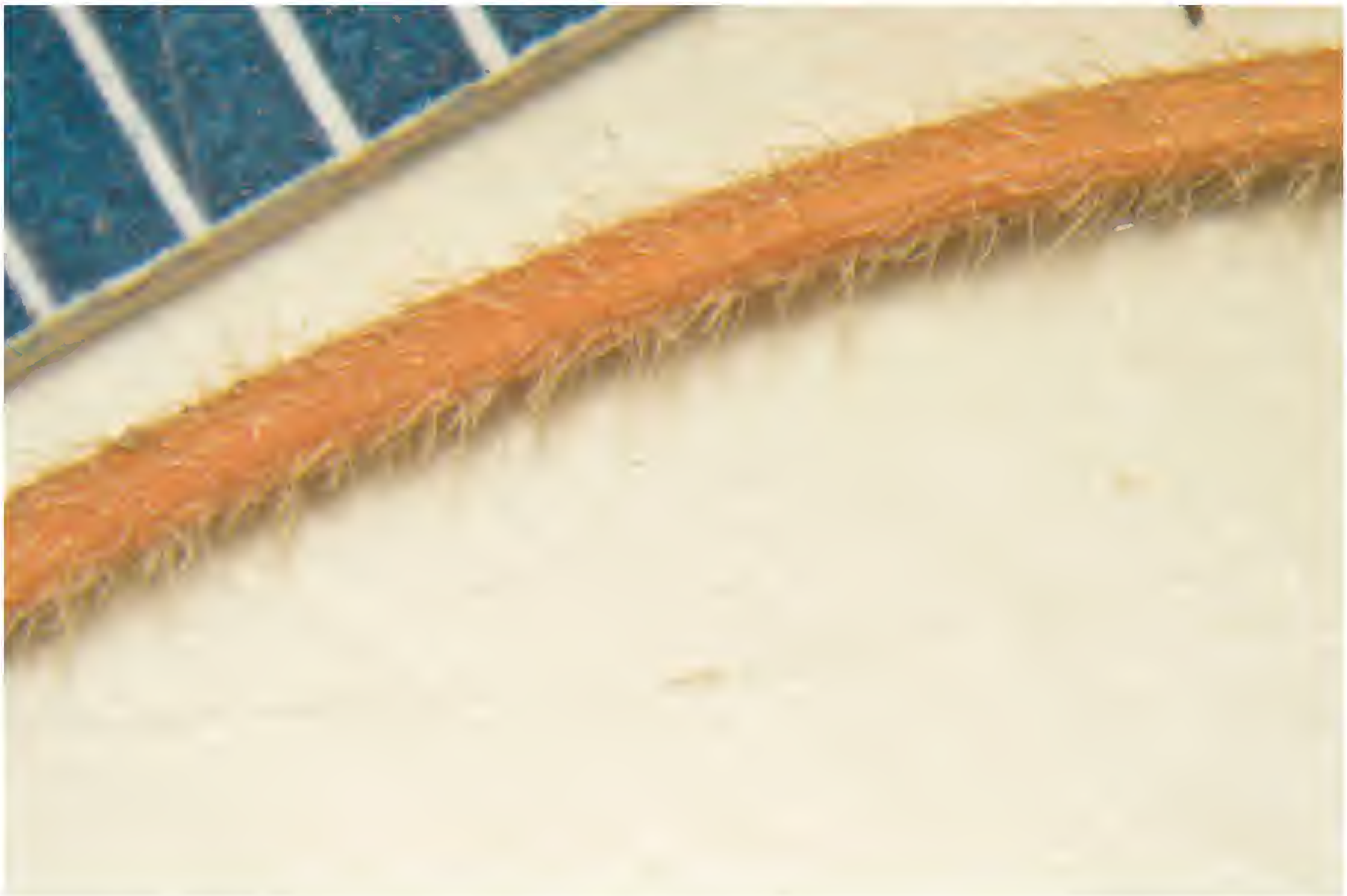


Figure 40. *Galactia volubilis*, with a retrorsely hirsute stem (*Caudle et al. 5744*). The distal portion of the stem is towards the right.

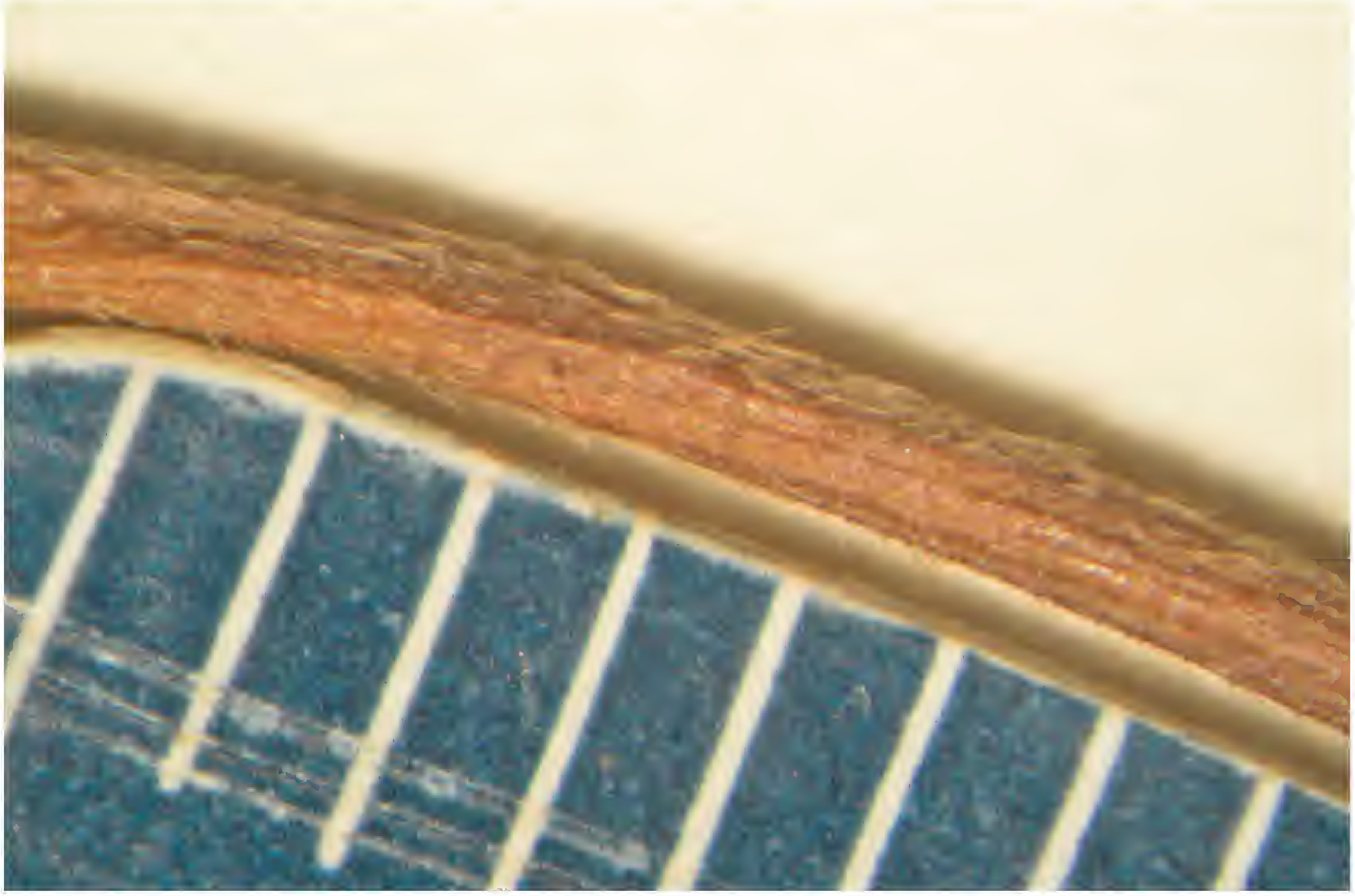


Figure 41. *Galactia volubilis*, with a retrorsely strigose stem (*Gandy MWSR0074*). The distal portion of the stem is towards the upper left.

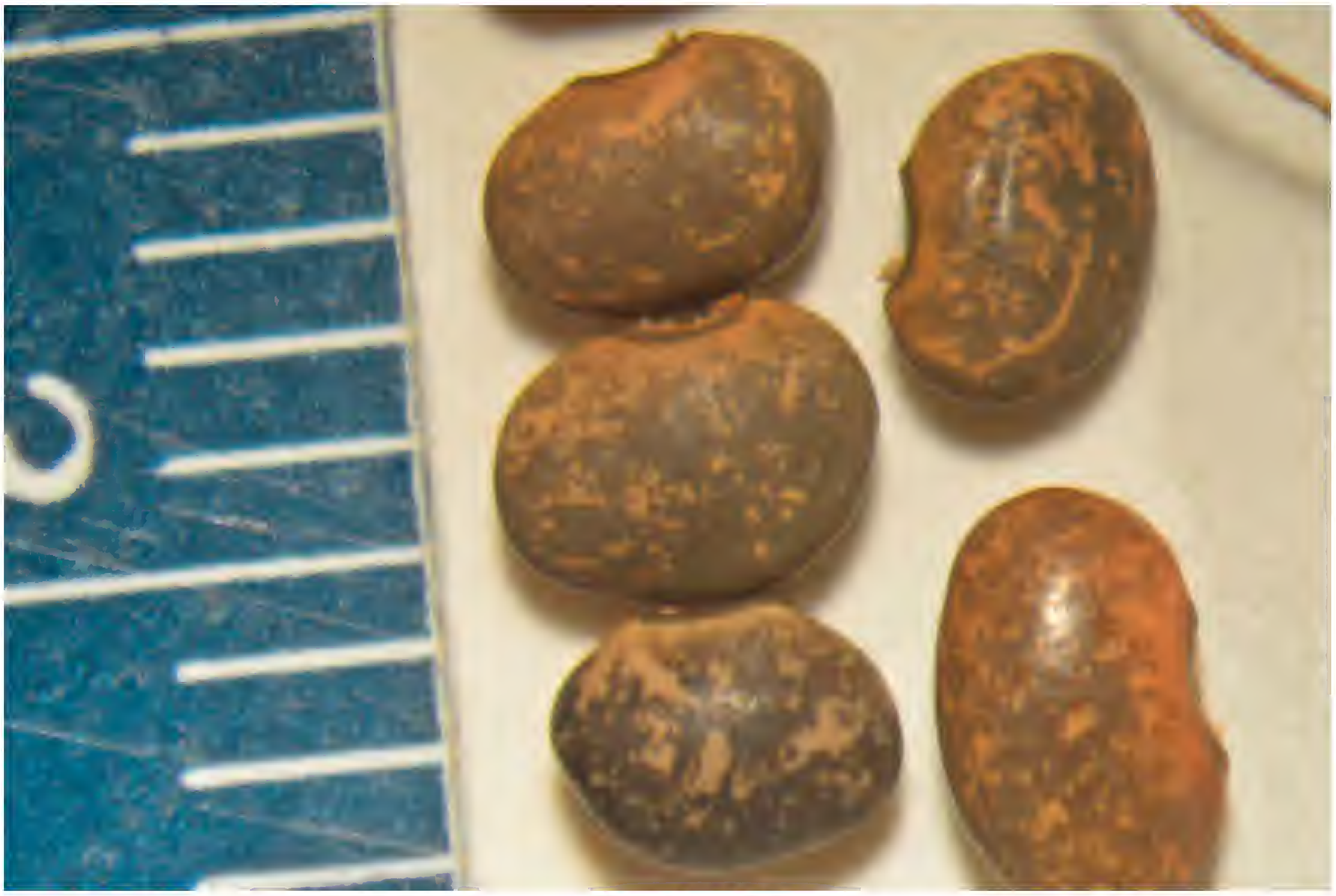


Figure 42. *Galactia volubilis*, seeds (*Hansen et al. 10840*).

Genetic and environmental influences on the yields of pentane extractable hydrocarbons of *Helianthus annuus* (Asteraceae, Sunflowers)

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ABSTRACT

Sunflowers (*H. annuus*) from natural populations in the Texas Panhandle and Salt Lake City, UT were analyzed for their % HC yields and g HC/g DW 10 leaves. Seeds from these populations were germinated and plants grown in the OPSU greenhouse to investigate the influence of the environment on HC yields. The ratio of % HC yields for greenhouse (GH) plants vs natural (Nat) plants was (GH/Nat): GT: 45.9%; LT: 55.6%; SLC: 78.3%). Plants from both of the populations in the Texas Panhandle (GT, Gruver, TX; LT, Lake Tanglewood, TX) had yields about 50% higher than their progeny grown under greenhouse conditions. Plants from these natural populations were severely damaged by grasshoppers, other insects and pathogens, as well as high winds and large variations in rainfall during the season (water stress). In contrast, the SLC (Salt Lake City, UT) population was an urban population that appeared to have much less insect damage to the leaves and no significant wind damage. Yields of HC (g/g leaf basis) were also much lower in greenhouse plants, but this is largely due to the lower biomass produced in small pots. Hybrids obtained by crossing two high yielding native sunflowers were greenhouse grown and these produced much less HC yields (4.59%, P1xP2, 4.91%, P2xP1) than found in their high yielding, natural habitat, parents (9.44 P1, 10.03 P2 %). These experiments indicate that HC yields from sunflower leaves are greatly induced (up to 55%) by stresses in the environment. Published on-line www.phytologia.org *Phytologia 99(2):186-190 (May 9, 2017)*. ISSN 030319430.

KEY WORDS: *Helianthus annuus,* Sunflower, greenhouse grown, field grown, stress induced hydrocarbon synthesis.

Recently, Adams et al. (2017) reported on geographic variation in pentane extractable hydrocarbons (HC) in natural populations of *Helianthus annuus* L. Yields of HC were highest in the Gruver, TX (GT, 7.99%) and Lake Tanglewood, TX (LT, 7.89%) populations. The leaves of these populations were severely damaged by grasshoppers, other insects and pathogens. It may be that insect damage (and wind damage, etc.) induced synthesis of defense chemicals that led to these high amounts of HC yields.

To test this effect, seeds were collected from these populations plus the Salt Lake City (SLC) population and germinated. The plants were then grown in a greenhouse and leaves harvested at stage R 5.1 - R 5.3 (as done in the field sampling study). The purpose of this paper is to present a comparison of the HC yields from natural and greenhouse (protected and sheltered) plants of *H. annuus* to examine the effects on HC yields when growing under quite different environmental conditions.

This is a part of a continuing study on the development of sunflowers as a source for natural rubber and bio-fuels from the biomass (Adams, et al., 1986; Adams and Seiler, 1984; Pearson et al., 2010a,b; Seiler, Carr and Bagby, 1991).

MATERIALS AND METHODS

Population locations for seed collections:
Lake Tanglewood, TX (LT) - Field notes:
2- 3 ft plants, lots of resin on petioles and leaf veins, many sugar ants (black ants), most with wilted leaves, very dry in July, common in native grass and on disturbed roadside, brush dump area, Lake Tanglewood, ~50% flowering, 35° 04' 23.7" N, 101° 47' 29.0" W, 3239 ft., Date: 12 July 2016, County: Randall; State: TX Coll. Robert P. Adams No. 14947

Gruver, TX (GT) - Field notes:
2-3' tall, 10% flowering, lots of damage to leaves by grasshoppers, etc., some with many sugar ants, copious resin at base of leaves, along fence row, on TX 206, 1-5:1.2 mi s, 6-10: 1.3 mi. s of Gruver, TX. 36° 14' 52" N, 101° 24' 52" W, 3161 ft, Date: 16 July 2016, County: Hansford; State: TX
Coll. Robert P. Adams No. 14952

Salt Lake City, UT (SLC) - Field notes:
next to sidewalk, flowering and seeding, multiple branches. common along sidewalks, Mill Creek, UT. s side of I80 on 2000 E, east side of 2000 E. 42° 52' 49" N, 112°' 25' 35" W, 4625 ft, Date: Sept. 3, 2016, County: Salt Lake; State: Utah. Coll. Robert P. Adams No. 15026

Bulk seed collections were made from LT, GT and SLC populations and the seeds stratified at 4°C for 1 week in a 1000 ppm GA3 solution (Adams and TeBeest, 2016, 2017), then placed on moist filter paper inside petri dishes. Seeds germinated in 10 - 14 days and seedlings were transplanted to potting soil in seed tube flats. After two weeks, the seedlings were transplanted into 7" round pots. The plants were grown the OPSU greenhouse were watering as needed with 12 hrs. supplemental light.

The lowest growing, non-yellowed, 8 mature leaves were collected at stage R 5.1-5.3 when the first flower head opened with mature rays when the HC yields are reported as highest for sunflowers (Adams et al. 2016). The leaves were air dried in paper bags at 49° C in a plant dryer for 24 hr or until 7% moisture was attained.

Leaves were ground in a coffee mill (1mm). 3 g of air dried material (7% moisture) were placed in a 125 ml, screw cap jar with 20 ml pentane, the jar sealed, then placed on an orbital shaker for 18 hr. The pentane soluble extract was filtered through a Whatman paper filter into a pre-weighed aluminum pan and the pentane evaporated on a hot plate (50°C) in a hood. The pre-weighed aluminum pan with concentrated hydrocarbon extract was weighed and tared.

RESULTS

Table 1 shows the biomass (DW, 10 leaves), % HC yields, and g HC/gDW 10 leaves for sunflowers growing at Gruver, Lake Tanglewood, and Salt Lake City from natural populations and for plants grown in the OPSU greenhouse. In general, the plants were much more robust in the field and the yields were much higher in nature than in the greenhouse.

These trends are shown graphically in Figure 1. The DW of 10 leaves from plants grown in the greenhouse was only 13% to 23% as much as field grown plants. Because the greenhouse plants were grown in 7" pots, this limited their growth. In addition, the greenhouse had a 50% shade cloth that limited the sunlight. Greenhouse sunflowers had elongated stems compared to natural field sunflowers.

Table 1. Yields of hydrocarbons (HC) *H. annuus*, from three natural populations and progeny obtained by growing field collected, bulk seed, then germinating and growing these progeny in the greenhouse. 2 x Standard error the mean computed as 2 x standard deviation / $(n)^{1/2}$. Xm = mean, 2Se = 2 x standard error of mean (95.6% of samples).

	naturally grown Xm±2SE			greenhouse grown Xm±2SE		
population sampled	g DW 10 lvs	% yield	g/ DW 10 lvs	g DW 10 lvs	% yield	g/ DW 10 lvs
14952 Gruver, TX	19.36 ± 2.010(40)	7.99± 0.537	1.499± 0.137	2.54± 0.178(60)	3.67± 0.249	0.092± 0.00798
14947 Lake Tanglewood, TX	19.11 ± 1.997(20)	7.88 ± 0.735	1.484 ± 0.200	2.79± 0.446(14)	4.38± 0.858	0.120± 0.0265
15026 Mill Creek, Salt Lake City, UT	11.92 ± 3.883(20)	5.75± 0.968	0.672± 0.195	2.69± 0.366(17)	4.50± 0.436	0.121± 00213

The ratio of % HC yields for greenhouse (GH) plants vs natural (Nat) plants was (GH/Nat): GT: 45.9%; LT: 55.6%; SLC: 78.3%, Fig. 1, Table 1). Progeny from both of the Texas Panhandle (GT, Gruver, TX; LT, Lake Tanglewood, TX) populations had yields about 50% lower when grown under greenhouse conditions. Plants from these populations were severely damaged by grasshoppers, other insects and pathogens as well as high winds and large variations in rainfall during the season (water stress). In contrast, the SLC (Salt Lake City, UT) population was an urban population that appeared to have much less insect damage to the leaves and no significant wind damage. Of course, it was subject to fluctuations in moisture.

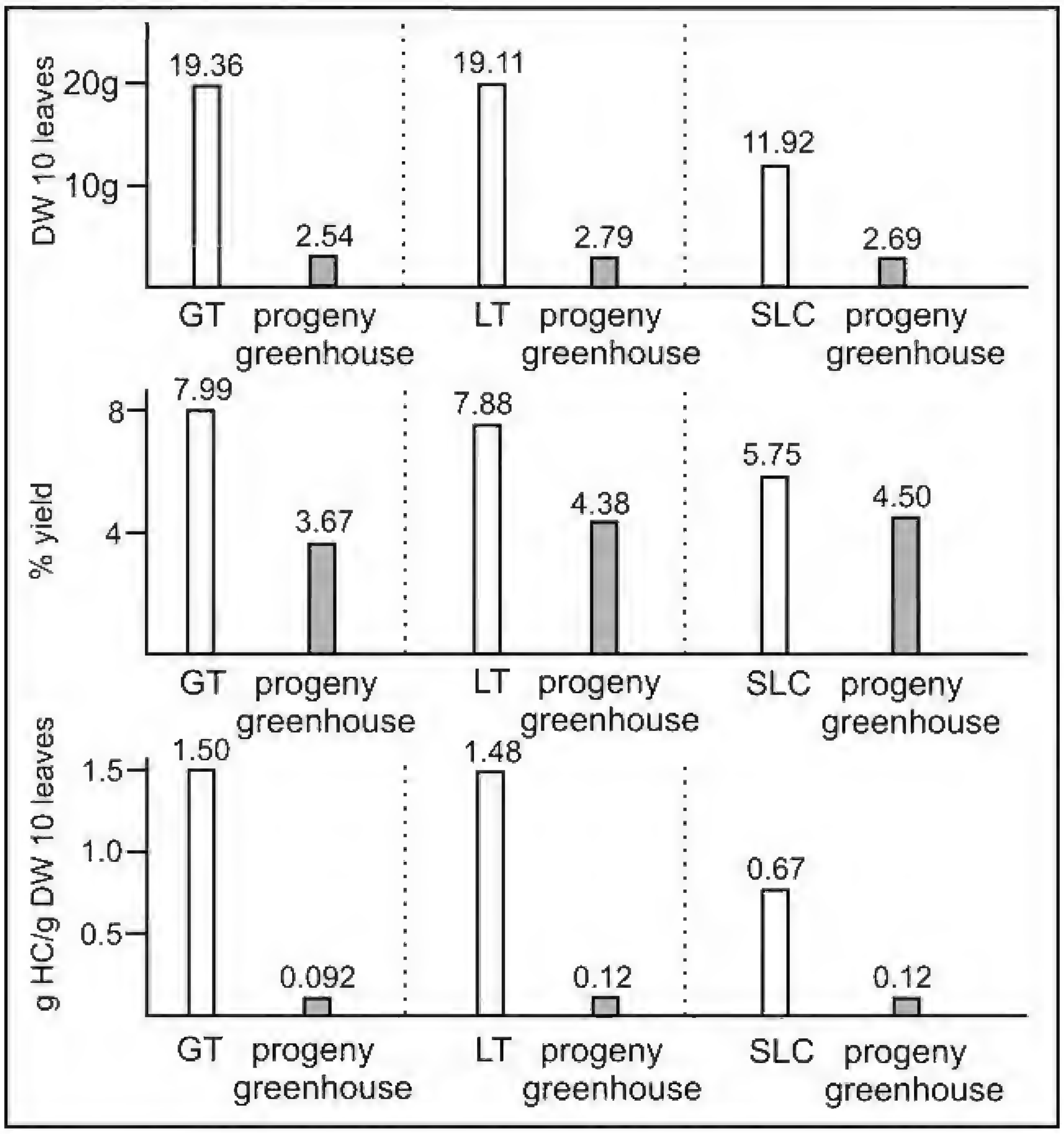

Figure 1. Comparisons of DW 10 leaves, % HC yield, and g HC/ g DW 10 leaves for field sampled sunflowers vs their progeny grown in the greenhouse at OPSU.

Hybrids produced by crossing two high yielding, native sunflowers (GT29, GT30, Gruver, TX), were grown in the OPSU greenhouse. These hybrid plants had much smaller yields (4.59%, 4.91% Table 2) than found in their high yielding, naturally grown parents (9.44, 10.03%, Table 2.). In addition, the hybrids (from the cross and the reciprocal cross) also had much lower HC concentrations (g HC/ g DW 10 lvs, Table 2).

Table 2. Production of HC from progeny of crossing high yielding individuals P1, GT 29 (9.44% HC, 1.417 g HC/ DW 10 leaves) and P2, GT 30 (10.03%, 0.917 g HC/ 10 leaves). Cross I = P1, GT29(male) x P2, GT30(female), Cross II = P1, GT29(female) x P2, GT30 (male). GT29 and GT30 were naturally growing *H. annuus* transplanted from the field in Gruver, TX, to the greenhouse. Crosses were made under controlled conditions in the greenhouse. Selfing in GT29 and in GT30 resulted in no seeds showing that these *H. annuus* are self-sterile. Progeny were grown in the greenhouse.

crosses	g DW 10 lvs	% yield	g/ DW 10 lvs
Parent 1, GT29	15.01g	9.44%	1.42g
Parent 2. GT30	9.14g	10.03%	0.92g
Cross I = P1, GT29(male) x P2, GT30(female) 26 hybrids	2.42g± 0.156	4.81%± 0.506	0.116g± 0.0149
Cross II = P1, GT29 (female) x P2 GT30 (male) 25 hybrids	2.97g± 0.257	4.59%± 0.450	0.139g± 0.020

The pattern of plants from the natural environment (with insect, pathogens and wind damage as well as moisture stress) having higher HC yields than plants from the protected greenhouse environment is shown in Figure 2. These data are consistent with the results previously shown (Table 1, Fig. 1) for field population samples vs. greenhouse grown plants from bulk seed collections.

Thus, it appears, in these cases, that up to 55% of the HC concentrations in natural populations of *H. annuus* in the Texas Panhandle are induced by the environment. The SLC (Salt Lake City) population was under less stress, but even that stress resulted in 22% greater HC concentration than in the non-stressed greenhouse plants.

Although these results are preliminary, they do show that growing sunflowers in a lush, sheltered environment (i.e., greenhouse) is not efficient for the production of high yields of HC. These results support the idea that much of the HC synthesis in sunflowers (up to 55%) is induced by stress to the plants. How much of that synthesis is due to insect and/ or pathogen damage vs. moisture stress is not known.

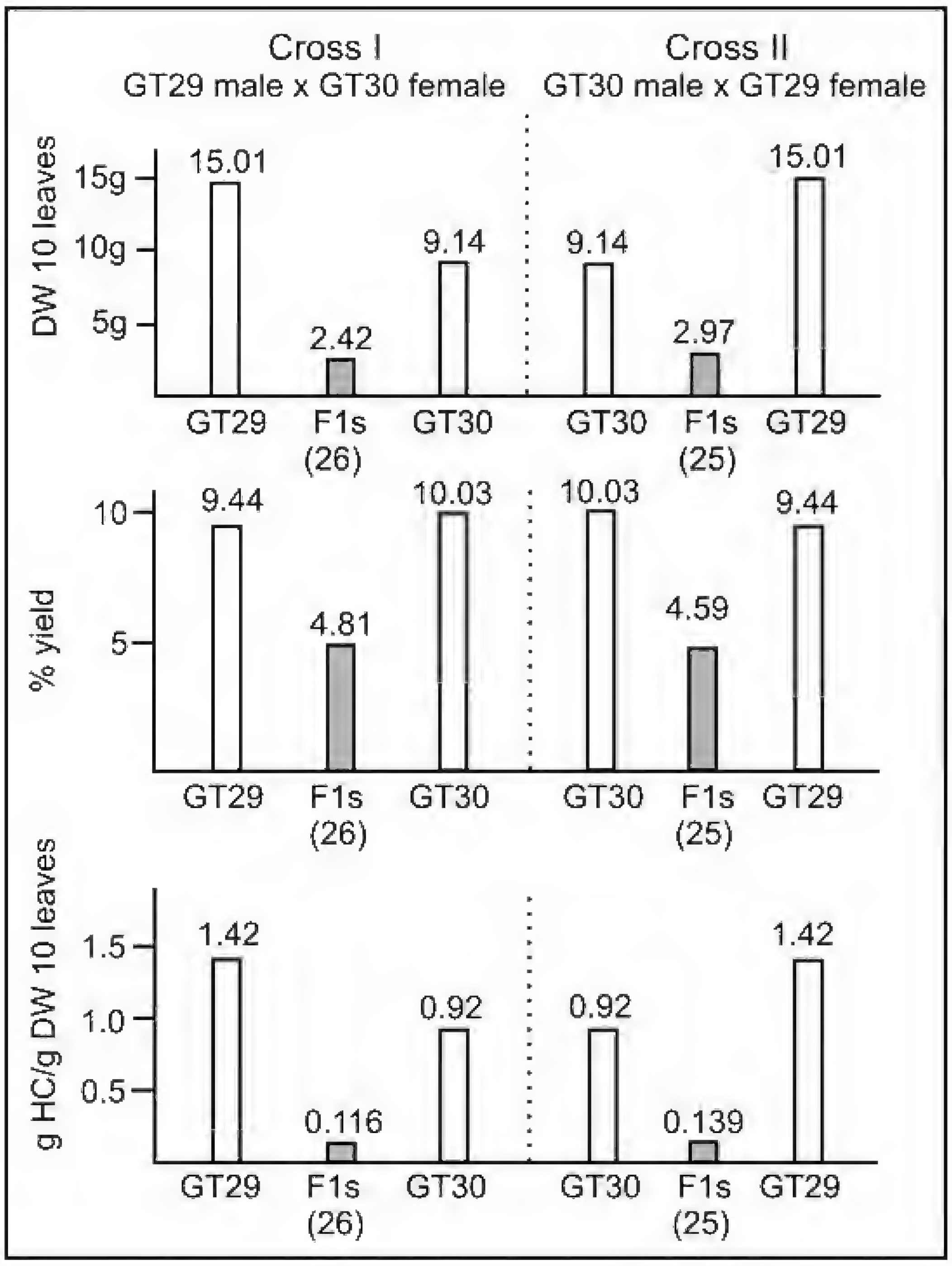

Figure 2. Comparison of DW 10 leaves, % HC yield, and g HC/g DW 10 leaves for field grown sunflowers (P1, GT29, P2, GT30) vs hybrids grown in the greenhouse at OPSU.

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